A REASSESSMENT OF THE PAPUAN SUBFAMILY ASTEROPHRYINAE (ANURA: MICROHYLIDAE)

by

THOMAS C. BURTON

Department of Zoology, University of Adelaide, Adelaide, South Australia 5000

ABSTRACT

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Information obtained from examination of the osteology, myology and external morphology is used in a phylogenetic analysis to assess the relationships in the Asterophryinae, a subfamily of terrestrial and fossorial microhylid frogs restricted to the Papuan Subregion, and to assess the relationships between the Asterophryinae and the other Papuan subfamily, Genyophryninae. While the Asterophryinae is monophyletic, no evidence of monophyly of the Genyophryninae is found. Taxonomic changes are made and all genera redefined in light of the phylogenetic analysis: four new tribes are erected to accommodate monophyletic groups of asterophryine genera; the genus *Mantophryne* Boulenger is resurrected to accommodate three species currently included in *Phrynomantis*; and *Xenorhina doriae* is transferred to *Phrynomantis*.

FIG. 1. Distribution of the Microhylidae (adapted from Savage, 1973).

INTRODUCTION

The Microhylids of the Papuan Zoogeographic Subregion

The frog family Microhylidae is distributed predominantly in the tropical areas of Asia, Africa, South America and the Australian Region, but with representatives also in the adjacent temperate areas of Asia, Africa and the Americas (Fig. 1). Frost (1985) lists 281 microhylid species, 61 genera and nine subfamilies, and the mean numbers of species per genus and of genera per subfamily are lower than in any other large family of frogs. The morphological diversity suggested by these figures reflects in part the ecological diversity found within the Microhylidae. There are fossorial, terrestrial, arboreal and aquatic species (Tyler 1976a), sharing the microhylid features of a firmisternal pectoral girdle, expanded sacral diapophyses, palatal folds, posteriorly directed process of the lower jaw (Roux 1944), *M. rectus abdominis pars anteroflecta* (Burton 1980) and a characteristic jawless tadpole (Parker 1934).

The subfamilial classification of the Papuan microhylids has long been contentious. In his monograph of the microhylids, in which he established the basis of the modern classification of the family, Parker (1934) recognized two Papuan subfamilies, Asterophryinae and Sphenophryninae. He recognized that these subfamilies were closely related and the only microhylids sharing the characteristic of direct development; as the distinctions between them were blurred by exceptions he expressed misgivings about separating them taxonomically: (a) while all sphenophrynines possessed a procoelous backbone, and nearly all of the asterophryines possessed a diplasiocoelous backbone, one asterophryine, *Genyophryne thomsoni* exhibited the sphenophrynine condition; (b) while the maxillae of all sphenophrynines were separated anteriorly by the premaxillae (the "eleutherognathine" condition), and nearly all of the asterophryines were symphygnathine, i.e., the two maxillae were fused on the midline anteriorly to the premaxillae, the three members of the genus *Metopostira*, *M. atra* (=*Barygenys atra*), *M. kopsteini* (=*Phrynomantis kopsteini*) and *M. ocellata* (=*Hylophorbus rufescens*)) and *G. thomsoni* exhibited the sphenophrynine condition. Parker considered, but rejected the advisability of classifying *G. thomsoni* as a sphenophrynine. *G. thomsoni* is a heavily built frog (as most asterophryines but few sphenophrynines are) and Parker considered the tongue of *G. thomsoni* to resemble the posteriorly adherent tongue of the asterophryines more than the sphenophrynine tongue, which is free posteriorly.

Zweifel (1971) and Savage (1973) independently tackled the problem of the unsatisfactory distinction between Asterophryinae and Sphenophryninae. Savage's solution was to declare the taxonomic distinction between these two subfamilies of direct-developing frogs "invalid". At the same time, echoing Noble (1931), he claimed that the Asian genus *Calluella*

(which is not direct-developing) "appears to be a primitive genus from which the more highly evolved asterophryines [=Asterophryinae + Sphenophryninae] may have developed", and so he included the Sphenophryninae and *Calluella* (*sensu* Inger, 1967) in an enlarged Asterophryinae.

Zweifel's solution was to examine the morphology of the animals, especially *G. thomsoni*, the species which had provided much of the heterogeneity in Parker's Asterophryinae. He found that in tongue morphology as in other features, *Genyophryne* resembled the sphenophrynines more than the asterophryines, and he transferred *G. thomsoni* into Sphenophryninae. Recognition that *G. thomsoni* was more closely related to the sphenophrynines allowed new diagnoses of two subfamilies which were consistently distinct for two characters: (1) Asterophryinae diplasiocoelous with adherent tongues, (2) Genyophryninae (Sphenophryninae plus *Genyophryne*) procoelous with tongues at least one-quarter free posteriorly; and mostly consistent for two others (almost all asterophryines with symphygnathine maxillae and dentaries; all genyophrynines with eleutherognathine maxillae and dentaries). (Zweifel 1981) and subsequent authors continued to refer to the augmented Sphenophryninae as Sphenophryninae, but Dubois (1985) indicates that Genophryninae Boulenger 1890 has priority over Sphenophryninae Noble 1931.) Zweifel (1972) considered Genyophryninae the parent group of the Asterophryinae. This implies that Genyophryninae is not a monophyletic sister-group but a paraphyletic parent-group. Subsequently, Tyler (1979) added to Zweifel's list of characters separating the subfamilies a character associated with the superficial submandibular musculature, viz., overlap of the *Mm. interhyoideus* and *intermandibularis* which he found present in all but one of the asterophryine genera and in no genyophrynines (*sensu* Zweifel, 1971) (Table 1). Tyler (1979) concurred with Zweifel's view that the Asterophryinae arose out of the Genyophryninae, and cited his study of the submandibular muscles (Tyler 1974) in support of this position.

TABLE 1. CHARACTERS TO DISTINGUISH THE ASTERO-PHRYINAE FROM THE GENYOPHRYNINAE (AFTER TYLER 1979)

Character	Asterophryinae	Genyophryninae
Maxillae	Often overlapping premaxillae, maxillae, and usually in contact	Not overlapping premaxillae. Never in contact medially
Dentaries	In contact anteriorly (except in *Hylophorbus*)	Not in contact
Vertebral column	Diplasiocoelous	Procoelous
Tongue	Subcircular, entirely adherent, often with a median furrow and posterior pouch	Oval, half-free behind, lacking median furrow and posterior pouch
Interhyoideus muscle	Anteriorly underlies *intermandibularis* (except in *Hylophorbus*)	Does not underlie *intermandibularis*

In this study I follow Zweifel's classification and the terms "Asterophryinae" and "asterophryine" are used in Zweifel's restricted sense. The species and genera which constitute the Asterophryinae are listed in Table 2.

The Asterophryinae currently comprises 43 named taxa in seven genera. These species occur exclusively within the Papuan Subregion, mainly on the island of New Guinea, but some occur on islands from Seram, Amboina and Halmahera in the west to the Louisiade Archipelago in the east. The Genyophryninae is also centred upon the New Guinea mainland but ranges far more widely, from the Philippines in the north to tropical Australia in the south, and from Sulawesi and the Lesser Sunda Islands in the west to New Britain and the Louisiade Archipelago in the east. All of the six genyophrynine genera (Table 3) occur on the island of New Guinea, and only three of these (*Cophixalus, Oreophryne* and *Sphenophryne*) occur elsewhere. Of approximately 70 species, 50 have been recorded from New Guinea (Zweifel and Tyler 1982).

TABLE 2. THE ASTEROPHRYINAE

Asterophrys Günther 1858
 turpicula (Schlegel) 1837

Barygenys Parker 1936
 atra (Günther) 1896
 cheesmanae Parker 1936
 exsul Zweifel 1963
 flavigularis Zweifel 1972
 maculata Menzies and Tyler 1977
 nana Zweifel 1972
 parvula Zweifel 1980

Hylophorbus Macleay 1878
 rufescens rufescens Macleay 1878
 r. extimus Zweifel 1972
 r. myopicus Zweifel 1972

Pherohapsis Zweifel 1972
 menziesi Zweifel 1972

Phrynomantis Peters 1867
 boettgeri (Mehely) 1901
 dubia (Boettger) 1895
 eurydactyla Zweifel 1972
 fusca Peters 1867
 glandulosa Zweifel 1972
 humicola humicola Zweifel 1972
 h. compta Zweifel 1972
 infulata Zweifel 1972
 kopsteini (Mertens) 1930
 lateralis (Boulenger) 1897
 louisiadensis (Parker) 1934
 personata Zweifel 1972
 robusta (Boulenger) 1898
 slateri (Loveridge) 1955
 stictogaster Zweifel 1972
 wilhelmana (Loveridge) 1948

Xenobatrachus Peters and Doria 1878
 bidens (van Kampen) 1909
 giganteus (van Kampen) 1915
 macrops (van Kampen) 1909
 mehelyi (Boulenger) 1898
 obesus Zweifel 1972
 ocellatus (van Kampen) 1913
 ophiodon Peters and Doria 1878
 rostratus Mehely 1898
 subcroceus Menzies and Tyler 1977

Xenorhina Peters 1863
 bouwensi (de Witte) 1930
 doriae (Boulenger) 1888
 minima (Parker) 1934
 oxycephala (Schlegel) 1858
 parkerorum Zweifel 1972
 similis (Zweifel) 1956

TABLE 3. GENERA OF THE GENYOPHRYNINAE

Chaerophryne	van Kampen 1915
Cophixalus	Boettger 1892
Copiula	Mehely 1901
Genyophryne	Boulenger 1890
Oreophryne	Boettger 1895
Sphenophryne	Peters and Doria 1878

Zweifel (1972) undertook a major revision of the asterophryines (*sensu* Zweifel, 1971). In that paper, Zweifel used characters of cranial osteology and external morphology, and erected two alternative phylogenetic trees to indicate intergeneric relationships (Fig. 2). These proposed phylogenies agree in
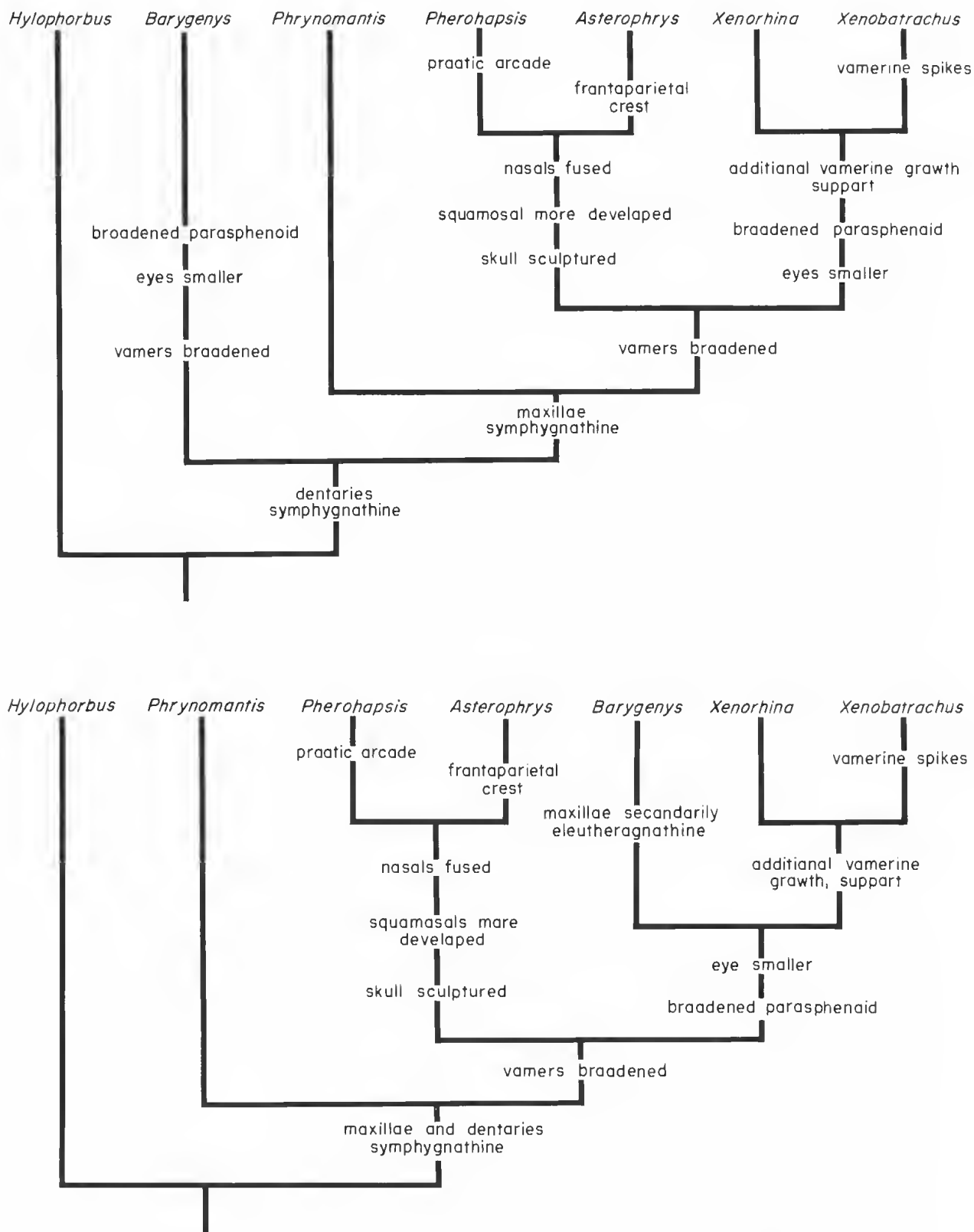

FIG. 2. Alternative proposed phylogenies of the Asterophryinae. Redrawn from Zweifel (1972, pp. 430, 431).

suggesting that *Hylophorbus* is the most primitive asterophryine genus, an hypothesis supported on the basis of features of the submandibular musculature by Tyler (1979). The proposed phylogenies differ in the placement of *Barygenys*, which is regarded as either a primitive genus which has undergone much parallel evolution with *Xenorhina* and *Xenobatrachus*, or a genus closely related phylogenetically to the other two, but which has undergone a reversal to partial eleutherognathy.

The Myology and Osteology of the Papuan Microhylids

The only published study of the entire musculature of any Papuan microhylid is that of Burton (1983a). Tyler (1974, 1979) and Emerson (1976a) examined the superficial throat musculature of some Papuan microhylids; Horton (1982) included in her review of tongue musculature one genyophrynine (*Sphenophryne robusta*); Trewavas (1933) examined the hyoid musculature of one genyophrynine (*Oreophryne celebensis*); Jones (1933) examined the pectoral musculature of four genyophrynines (*Cophixalus verrucosus, Genyophryne thomsoni, Oreophryne variabilis* and *Sphenophryne cornuta*); and Fry (1917) and Zweifel and Allison (1982) examined aspects of the musculature of *Cophixalus pansus*.

While osteological features were used by Boulenger (1882) and van Kampen (1923), the main osteological studies of Papuan microhylids are those of Mehely (1901), Wandollek (1910) and Zweifel (1971, 1972). Important contributions have also been made by Noble (1931), Parker (1934, 1936), Brongersma (1953) and Menzies and Tyler (1977).

Mehely (1901) described in detail the osteology and in particular cranial osteology of the following Papuan microhylids (Mehely's names in parentheses): *Phrynomantis (Mantophryne) lateralis, P. (Gnathophryne) boettgeri, P. (G.) dubia, P. (G.) robusta, Hylophorbus rufescens (Metapostira ocellata), Xenobatrachus rostratus (Xenorhina rostrata), Xenorhina oxycephala, Cophixalus (Phryxinalus) biroi, C. (P.) montanus, Copiula fistulans (C. oxyrhina), Oreophryne (Sphenophryne) biroi, O. celebensis, O. moluccensis (O. senckenbergiana), Sphenophryne mehelyi (Chaperina fusca)* and *S. (C.) polysticta.*

Wandollek (1910) described the osteology and illustrated the cranial bones and hyoids of *Choerophryne (Copiula) rostellifer, Oreophryne biroi (Mehelyia affinis* and *M. lineata), Sphenophryne cornuta, S. macrorhyncha (Chaperina quatuorlabata)* and *S. schlaginhaufeni).*

Noble (1931) and Parker (1934, 1936) included a small number of skeletal characters in their generic and subfamilial diagnoses; Brongersma (1953) described the skeleton of *Asterophrys turpicula;* Zweifel (1971) used some skeletal characters in his analysis of the relationships of *Genyophryne;* and Menzies and Tyler (1977) described osteological features of a number of

burrowing Papuan microhylids of the genera *Barygenys, Choerophryne, Copiula* and *Xenobatrachus.*

In his revision of the Asterophryinae, Zweifel (1972) relied to a large extent on cranial osteology. He described general features of the skeletons of asterophryines, the diagnostic features of each genus in generic accounts, and particular features of some species in species accounts. Zweifel's account of the cranial skeletons of asterophryines is comprehensive but scattered, and the contributions of the present study to the knowledge of the cranial skeleton are the addition of a few previously unrecorded features, and also information on a number of species not examined by Zweifel. This permits reinterpretation of some cranial characters.

There are problems in the interpretation of the cranial skeletons of asterophryines and in the selection of characters for phylogenetic analysis. The problems of interpretation arise from a number of factors: in all asterophryines there are some bones that are fused; in some asterophryines many bones are fused; and in some asterophyrines the task of discriminating bone margins is further complicated by exostosis.

The most problematic bone of the microhylid skull is the product of fusion of the vomer and the palatine. Mehely (1901) interpreted a narrow anterad projection of this bone skirting the medial margin of the choana as a vomer, and the remainder as a palatine. Noble (1931) and Parker (1934) referred to the entire bone as a prevomer and Zweifel (1972) as a vomer. The presence of odontoids on this bone convinced Noble and Parker (1926) that the bone was not a palatine, and they interpreted cases of separation of the anterad process from the rest of the bone as division of the prevomer, rather than separation of the prevomer from the palatine. I prefer to follow Trueb (1973) in regarding the identity of the bone as insoluble until ontogenetic data become available, and follow her in referring to this bone as a "vomero-palatine".

The most problematic species is *Pherohapsis menziesi*, the skull of which is heavily fused and exostosed, and particularly difficult to interpret in the absence of ontogenetic data. As myological and external similarities of *Pherohapsis* to *Hylophorbus*, three species of *Phrynomantis* and to a lesser extent *Asterophrys* indicate a close relationship with those taxa, I interpret the cranial structures of *Pherohapsis* as homologous with structures in those frogs. For example, I interpret the prootic arcade of *Pherohapsis*, a ribbon of dermal bone which forms an arch between the frontoparietal and the squamosal (Fig. 17), as a mediad extension of the posterad projection of the zygomatic ramus of the squamosal exhibited only by *Asterophrys, Hylophorbus* and the three *Phrynomantis* species. Similarly, although the dorsal surface of the otic capsule is so fused and featureless that it is impossible to identify individual bones, the

conformation of that surface and the adjacent broad medial flange of the squamosal shaft is consistent with the interpretation that at least part of the bone covering the otic capsule is an otic ramus of the squamosal. The dorsal surface of this otic ramus is continuous with the anterior surface of the medial flange of the squamosal shaft. This interpretation is comparable to the condition in *Asterophrys, Hylophorbus* and the three *Phrynomantis* species.

The post-cranial skeleton of asterophryines has been considered too uniform to be informative of relationships within the subfamily (Zweifel 1972, p. 428). In contrast, the post-cranial skeleton provides characters fundamental to the separation of the Asterophryinae and Genyophryninae (nature of the vertebral column), and to the diagnosis of genyophrynine genera (nature of the pectoral girdle).

Following Zweifel's revision of the Asterophryinae, a number of papers have appeared focussing on variation in the post-cranial skeleton of frogs. Trueb (1973) provided a useful survey of skeletal characters and subsequently demonstrated the use of measurements of skeletal features (Trueb 1977). Andersen (1978) surveyed variation of the manus and pes, and Tyler (1976b), Emerson (1979), Emerson and DeJongh (1980) and Emerson (1982) demonstrated and evaluated characters of the pelvic girdle. As a result of these studies more information and hypotheses relating to post-cranial skeletons are available to systematists.

Ecology of the Papuan Microhylids

The Papuan microhylids are diverse ecologically. Menzies (1975) uses four categories to accommodate the common species; to these Zweifel and Tyler (1982) add a fifth to accommodate some less common species. These categories are (a) fossorial, the frogs are normally found below ground from whence they call, rarely or never encountered on the surface: *Barygenys, Xenobatrachus* and probably *Xenorhina* (Menzies' placement of *Xenorhina* among the terrestrial genera is based on the only common *Xenorhina* species, *X. doriae*, which is shown in this study to be more appropriately assigned to *Phrynomantis*), *Choerophryne* and *Copiula* (Menzies and Tyler 1977), and probably *Genyophryne* (Zweifel 1971); (b) terrestrial, hiding under the ground by day, but moving about on the ground at night: *Asterophrys, Hylophorbus, Pherohapsis, Phrynomantis*, some species of *Cophixalus*, e.g., *C. pansus* (Zweifel and Allison 1982), some species of *Sphenophryne*; (c) scansorial, climbing low vegetation to two or three metres: some species of *Cophixalus* and *Sphenophryne*; (d) arboreal, climbing high into the trees: some species of *Cophixalus, Oreophryne*; (e) aquatic: *Sphenophryne palmipes* (Zweifel 1956).

Menzies stresses that there is overlap between these categories, and that it is arbitrary to a degree. Moreover, little is known of the ecology of the majority of species;

but it is clear that the asterophryines are far less diverse ecologically than the genyophrynines.

The terrestrial and fossorial frogs of both subfamilies burrow head first (Menzies and Tyler 1977). The frogs I observed in captivity (*Barygenys flavigularis, Phrynomantis lateralis, P. wilhelmana, Copiula fistulans, Cophixalus kaindiensis, Sphenophryne fryi, S. schlaginhaufeni*) conform with this mode of burrowing, the driving power coming mainly from the hind legs, the arms being used mainly to part leaf litter and moss. This mode of burrowing contrasts with that of other frogs which are described as burrowing head first, *Hemisus marmoratus* (Emerson 1976b) and *Arenophryne rotunda* (Tyler et al. 1984), both of which propel themselves largely by arm movements (Emerson 1976b, pers. obs.).

Aims of this Study

This study arose out of the observation by Tyler (1974) of diversity in the superficial throat musculature of the asterophryines. It was believed that a detailed comparative myological study might not only aid in the evaluation of Zweifel's (1972) phylogenetic hypotheses but also provide characters with which to evaluate the hypotheses of relationships between the two New Guinea subfamilies. Moreover, as differences were observed between Zweifel's (1972) drawing of the ilium of *Phrynomantis louisiadensis* and the ilia of several genyophrynines stored as alizarin preparations in the Department of Zoology, University of Adelaide, the potential usefulness of examination of the post-cranial skeleton was realized. Finally, unremarked heterogeneity in Zweifel's diagrams of skull morphology suggested that reassessment of skull characters might also yield useful characters.

The aims of this study have been to determine the relationships of the asterophryine genera, using characters of myology and osteology, and to contribute to the assessment of the merits of uniting the asterophryines and genyophrynines into a single subfamily.

MATERIALS AND METHODS

Material Available

The course of this study was dictated in part by the availability of material. Specimens of adult asterophryines available for dissection are often difficult or impossible to obtain. Of the 40 taxa examined by Zweifel (1972), 18 were represented in collections by fewer than 10 specimens each, and the three species named subsequently are known only by their type series. Although additional specimens of some of the very rare species have been collected since 1972, none has become commonly represented in collections. As a result there are a number of species unavailable for dissection and skeletal preparation.

As asterophryines undergo direct development and eggs of most species are hidden in leaf litter, under

moss or under logs, the discovery of eggs or larvae is rare and accidental. As asterophryines are very difficult to rear from the eggs to adulthood, identification of eggs generally is impossible unless an attendant adult is found; even then the evidence of identity is circumstantial. There are no published accounts of complete life histories of asterophryine larvae (Tyler 1976a), and larval material is so limited that a comparative study is impossible.

Techniques such as gel electrophoresis, karyology and microcomplement fixation are possible only when freshly killed specimens are available. It was impossible to obtain adequate samples from New Guinea to use any of these techniques.

Material Examined

A total of 268 specimens of preserved adult microhylids were examined, including 196 specimens of 33 species or subspecies of asterophryines, representing all seven genera. Of the 268 specimens, 256 were examined externally, 159 specimens (114 asterophryines) were dissected, at least partially, for myological examination, 115 specimens (82 asterophryines) were cleared and stained for osteological examination, 16 dried skeletons (10 asterophryines) were prepared, and x-rays were obtained of 37 specimens (all asterophryines). Three specimens (AUZ A206, 207, 208) had previously been cleared and stained.

A total of 23 specimens of preserved adult ranoids were examined externally, and partially dissected for myological examination. These specimens represent two families, 10 genera and 14 species. All are uncatalogued specimens housed in the Department of Zoology, University of Adelaide: Ranidae — *Cacosternum* sp. (1 specimen), *Hemisus marmoratus* (1), *Natalobatrachus* sp. (1), *Platymantis papuensis* (1), *Pyxicephalus* sp. (2), *Rana fuscigula* (1), *R. grayi* (1), *R. grisea* (5), *R. papua* (1); Hyperooliidae — *Afrixalus* sp. (2), *Hyperolius marmoratus* (2), *H. tuberilinguis* (1), *Kassina* sp. (2) and *Leptopelis* sp. (2).

The specimens were preserved in 65% or 70% ethanol. Most were lent by the institutions listed. Others collected on a field trip are lodged in the collection of the Department of Zoology, University of Adelaide. These specimens were killed in a 3% chloral hydrate solution, fixed in 3% formalin, and preserved in 65% ethanol.

Specimens Examined

Abbreviations: AA: Collection of Dr A. Allison, Wau Ecology Institute, PNG; AM: Australian Museum, Sydney; AMNH: American Museum of Natural History, New York; AUZ: Department of Zoology, University of Adelaide (unregistered apart from skeletal preparations); BPBM: Bishop Museum, Honolulu; FMNH: Field Museum of Natural History, Chicago; MCZ: Museum Comparative Zoology, Harvard; RMNH: Rijksmuseum van Natuurlijke Historie, Leiden; SAMA: South Australian Museum, Adelaide; UPNG: Biology Museum, University of Papua New Guinea, Port Moresby.

ASTEROPHRYINAE

Asterophrys turpicula (9) Vogelkop: RMNH 16655; Olsobip: UPNG 1548; Megalsimbip, Ok Menga: UPNG 6739-45.

Barygenys atra (8) Lejo via Popondetta: UPNG 3831, 3832, 3836, 3837, 3957, 3958, 5475, 5476.

Barygenys exsul (1) Alotau: UPNG 5201.

Barygenys flaviguluris (7) Mt Kaindi: AUZ A729; B726a, B726b, B728, D741, SAMA R23851, UPNG 5134.

Barygenys maculata (11) Agaun: UPNG 5091-99, 5101, 5102.

Barygenys nana (4) Fungoi, Kaironk Valley, Schrader Mts: AM 22802; Kaironk Valley, Schrader Mts: UPNG 3245, 3247; Elimbari: UPNG 3249.

Barygenys sp. nov. (6) Mt. Missim: AA 11171, 11172, BPBM 9366-69.

Hylophorbus r. rufescens (11) Baiyer River: AUZ A722, D738; SAMA R23844; Madang: UPNG 2285, 2286, 2288; Agaun: UPNG 5041, 5042, 5044; Manga, Huon Pen: UPNG 5714; Go River, Huon Pen: UPNG 5732.

Hylophorbus r. extimus (1) Mt Riu, Sudest I.: AMNH 60092.

Hylophorbus r. myopicus (1) Kulumadau, Woodlark I.: AMNH 59988.

Pherohapsis menziesi (6) Sogeri: UPNG 1865, 1970, 2093, 2578, 2579, 5196.

Phrynomantis eurydactyla (2) Kahilfon, Bultem: UPNG 5306-07.

Phrynomantis fusca (1) Rohua, S. Seram: UPNG 5257.

Phrynomantis h. humicola (18) Kotuni, Mt Otto: AMNH 66266-70 (2 specimens); Daulo Pass: MCZ 52970-81, 52983-86.

Phrynomantis h. compta (3) Kaironk Valley, Schrader Mts: SAMA R9387 (3 specimens).

Phrynomantis infulata (3) Arau, Kratke Mts: AMNH 66685, 66699, 66670.

Phrynomantis lateralis (13) Taraka via Lae: AUZ A730, B724a, B724b, D737, SAMA R23838; Lae: MCZ 59000; 16 km S of Popondetta: MCZ 87535; McDowell I., Purari R.: UPNG 2499, 2500; Alotau: UPNG 2619, 2621, 2622, 5202.

Phrynomantis louisiadensis (5) Mt Rossel, Rossel I.: AMNH 60135-43 (2 specimens); Rossel I.: AMNH 89117; Abaleti, Rossel I.: AMNH 69347, UPNG 5689.

Phrynomantis personata (2) Lumi: AMNH 78092; Rauit: UPNG 4087.

Phrynomantis robusta (4) Derongo: MCZ 81688; SAMA R10580; Siagara, Misima I.: UPNG 4295; Bwagaoia, Misima I.: UPNG 4303.

Phrynomantis stictogaster (17) Lufa Patrol Post: MCZ 59908-16; Okapa: SAMA R20886-93.

Phrynomantis wilhelmana (16) Wahgi-Sepik Divide:

AM R16825; Daulo Pass: AM R66747; Eastern slopes of Mt Wilhelm: AMNH 65868-86 (2 specimens); Tomba: AUZ A727, B721(a), B721(b), B723, B731; Mt Giluwe: SAMA R23849; Kogi, Suai Ra: MCZ 59891-96.

Xenobatrachus giganteus (4) Eipomek Valley: UPNG 5346, 5347, 5679, 5680.

Xenobatrachus mehelyi (6) Derongo: MCZ 81673, 81674; Imigabip: MCZ 81675, 81676; Tabubil: UPNG 4790; no data: AUZ.

Xenobatrachus obesus (3) 20 km NE of Lumi: AMNH 78187-207 (2 specimens); Amanab: UPNG 2822.

Xenobatrachus rostratus (1) Kaironk Valley, Schrader Mts: SAMA R9386 (4 specimens), UPNG 3240, 3244, 3342, 5014; Eipomek Valley: UPNG 5681, 5682.

Xenobatrachus subcroceus (5) Lae: UPNG 4390-93, 4143.

Xenorhina bouwensi (10) Kigonmendip, Ok Sibil Valley, Star Mts: RMNH 16657 (5 specimens), 16658 (5 specimens).

Xenorhina doriae (4) Mt Lamington: AM R9604; Camp III, Nimi R.: MCZ 64405; Bomai: SAMA R6284; Alotau: UPNG 2608.

Xenorhina minima (2) Eipomek Valley: UPNG 5677, 5737.

Xenorhina oxycephala (3) S. coast of Humboldt Bay: RMNH 5032; Fak-Fak: RMNH 17017; Eipomek Valley: UPNG 5678.

Xenorhina parkerorum (1) Halalinja, Nipa: UPNG 5827.

Xenorhina similis (1) Lake Habbema, Bele R., 18 km N: AMNH 43726.

GENYOPHRYNINAE

Choerophryne rostellifer (1): Moiyokabip Village, Bultem: UPNG 4410.

Cophixalus darlingtoni (2) Tomba, Mt Hagen: AUZ B735, SAMA R23844.

Cophixalus kaindiensis (1) Mt Kaindi: AUZ.

Cophixalus neglectus (3) Mt Bellenden Ker, Qld: AUZ A744, A747, B749.

Cophixalus ornatus (5) S. Bell Peak, Malbon Thompson Ra, Qld: AUZ A720, B725(a), B725(b), D740, SAMA R23845.

Cophixalus pansus (3) Bulldog Rd, Wau: AUZ (2 specimens), AUZ A209.

Cophixalus parkeri (2) Okapa: SAMA R5604 (2 specimens).

Cophixalus riparius (4) Okapa: SAMA R5216 (4 specimens).

Cophixalus shellyi (2) no data: AUZ (2 specimens).

Cophixalus variegatus (8) Mt Kaindi: AUZ B719, B743, D739, SAMA R23839-43.

Cophixalus verrucosus (3) Sogeri: AUZ (3 specimens).

Copiula fistulans (5) Lae: AUZ A723, D742, SAMA R23836, R23837; Agenchambo via Popondetta: SAMA R14241.

Genyophryne thomsoni (4) Agaun: AUZ (1 specimen), UPNG 5118, 5120, 5130.

Oreophryne biroi (1) Karimui: SAMA R10899.

Oreophryne insulana (2) Ma-u R., Camp I: AUZ B745, UPNG 3556.

Sphenophryne cornuta (1) Kigonmendip, Sibil Valley: SAMA R11599.

Sphenophryne fryi (5) S. Bell Peak, Malbon Thompson Ra, Qld: AUZ A746, B734, D736, SAMA R23854-55.

Sphenophryne robusta (4) Boonjie, 16 km SE of Malanda, Qld: AUZ (1 specimen), AUZ A208; Millaa Millaa, Qld: AUZ (1 specimen), AUZ A207.

Sphenophryne sp. (2) Wau: BPBM 9879, 9882.

Sphenophryne schlaginhauferi (2) Trauna Ridge, 13 km NE of Baiyer River, AUZ B733, SAMA R23852.

BREVICIPITINAE

Breviceps mossambicus (2) Bronkhorstbrust, S. Africa: AUZ.

Breviceps sp. (1) Durban N., S. Africa: AUZ.

DYSCOPHINAE

Calluella guttulata (1) Kuala Tahan, Pahang, Malaya: FMNH 143960.

MICROHYLINAE

Chaperina fusca (1) Deramakot, Kinabatangan Dist, N. Borneo: FMNH 77253.

Elachistocleis sp. (4) Tunapuna, Trinidad: AUZ (3 specimens), AUZ B748.

Glyphoglossus molossus (1) Sakaerat, Ampho Pak Thong Chai, Nakhon Ratchasima Prov., Thailand: FMNH 182650.

Kalophrynus pleurostigma (1) Nanga Tekalit Camp, Mengiong R., Kapit Dist, Sarawak: FMNH 138052.

Kaloula pulchra (1) Siracha, Chalemlarb, Chon Buri, Thailand: FMNH 175952.

Microhyla heymonsi (1) Bukit Lanjan, Selangor, Malaya: FMNH 186029.

Microhyla pulchra (1) Sakaerat, Amphoe Pak Thong Chai, Nakhon Ratchasima Prov., Thailand: FMNH 183064.

Methods: Morphology

External examination included the taking of standard measurements of snout-vent length (S-V), head width (HW), eye diameter (E), eye to naris distance (E-N), internarial span (IN), tympanum diameter (T), and tibiofibula length (TL). The measurements were taken with Mitutoyo dial calipers according to the methods described by Zweifel (1972). In 188 specimens the following additional measurements were taken: (a) head length (HL), the distance from the tip of the snout to the angle of the jaw (Fig. 3A); (b) mouth width (MW), the distance between the corners of the mouth (Fig. 3B); (c) mouth length (ML), the distance between the most anterior point of the mouth and the posterior corner (Fig. 3C).
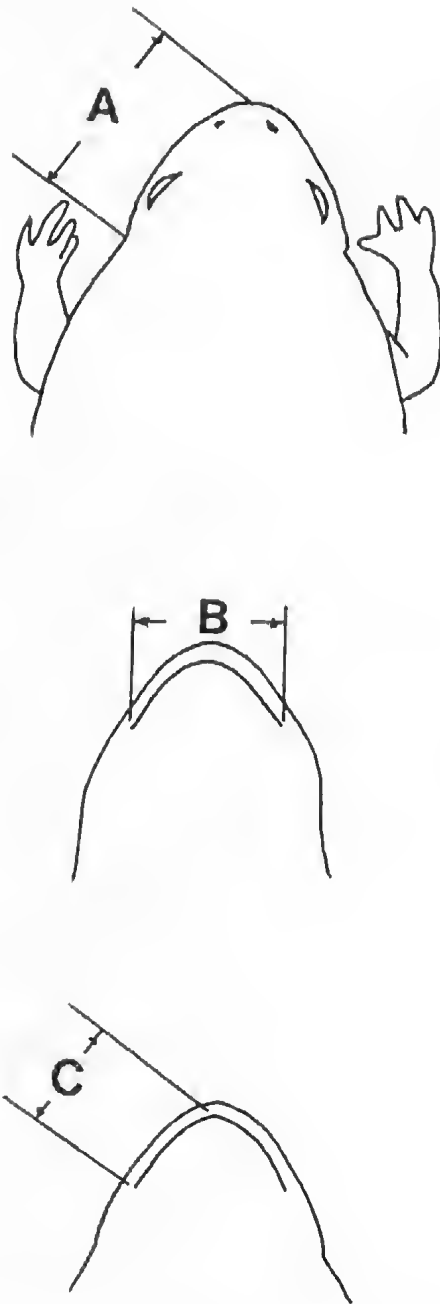
FIG. 3. Methods of measurement: A, head length; B, mouth width; C, mouth length

Myological dissections were carried out with the assistance of topical applications of the iodine-potassium iodide solution of Bock and Shear (1972). In cases where muscles were obscured by connective tissue, the tissue was bathed in 30% nitric acid until the connective tissue was removed, and the nitric acid was then aspirated. In 134 specimens all of the skeletal musculature was examined. In 32 specimens of rare species, dissection was prohibited, but partial examination of the muscles was carried out through pre-existing incisions made by previous workers. One rare specimen, *Phrynomantis fusca* UPNG 5257, was partly dissected through straight incisions in the skin, which was then folded back, and muscle groups

previously known to be taxonomically significant were examined.

The tongues and associated musculature of six specimens were examined histologically. Transverse sections were stained with Mayer's haematoxylon and eosin.

Muscle descriptions follow the terminology of Ecker (1889) as modified for the throat by Tyler (1971), the jaw by Starrett (1968), the hyolaryngeal apparatus by Trewavas (1933), the pectoral girdle by Jones (1933), the forearm and manus by Gaupp (1896), the pelvic girdle by Dunlap (1960) and cutaneous muscles by Burton (1980).

One hundred and one specimens were cleared and double-stained for skeletal examination by the Alcian blue-Alizarin red technique of Dingerkus and Uhler (1977). Seventeen specimens were cleared and stained with Alizarin red by the technique of Davis and Gore (1947) to reveal bones. Sixteen specimens were flensed, cleared of adherent soft tissue by application of sodium hypochlorite solution, and allowed to dry slowly. Thirty-seven specimens, most of them too rare to dissect, were radiographed from several aspects and prints obtained on a Rank Xerograph in positive mode.

As the drying process led to some collapse of skulls and caused some bones which are not articulated in cleared and stained specimens to come into contact, the osteological descriptions are based primarily on cleared and stained specimens. Osteological descriptions follow the nomenclature of Trueb (1973).

The skeletal preparations were surveyed in order to evaluate the potential for taking measurements in the manner of Trueb (1977). This survey indicated that the features with the best potential for yielding information regarding relationships were the angle between the vertebral column and the leading edge of the sacral diapophysis, the sacral expansion and the angle between the ilial shafts. These were measured using a goniometer attachment on a Wild M5 stereomicroscope, care having been taken that the features being measured were lying in a horizontal plane.

All myological and osteological drawings were prepared with the use of a Wild M5 stereomicroscope with an attached camera lucida.

Methods: Phylogeny

The approach adopted in this study is that of Hennig (1966) as defined by Wiley (1976). This involves the attempt to falsify competing hypotheses of recency of common ancestry of groups of taxa, using as evidence the distribution among the taxa of synapomorphies, that is, shared uniquely derived character states. The myology, osteology and external morphology of the asterophryines, genyophrynines and the other micro-hylids examined provided the characters that were the basis of the phylogenetic analysis.

There are a number of problems associated with the recognition of synapomorphy: first, the determination of primitive and derived character states, second,

distinction of cases where a shared derived character state has arisen once in a common ancestor (i.e., are "homologous" *sensu* Bock, 1963) from cases where similar character states have arisen independently in different lineages (i.e., are "homoplasious" *sensu* Bock, 1963), and third, how to handle cases of conflicting evidence of synapomorphy.

The problem of character state polarity has been addressed frequently in recent papers, e.g., Crisci and Stuessy (1980), De Jongh (1980), Stevens (1980, 1981), Arnold (1981), Bock (1981), Watrous and Wheeler (1981) and Wheeler (1981). In these papers many criteria have been assessed and, while a consensus has not emerged, the case favouring the use of outgroup analysis alone is compelling. That is, useful information regarding the direction of change can only be derived from analysis of the distribution of those states between the group under study and an outgroup. A character state shared by members of the group under study and the outgroup is considered primitive relative to a character state found only in some members of the group under study. The character state shared by members of the study group and the outgroup is assumed to have arisen in a common ancestor of the two groups, while the restricted character state is assumed to have arisen more recently in an ancestor common only to those species which share the state.

The outgroup method is by far the most widely used method of assessing character state polarities. Studies, including those of Marx and Rabb (1970), Lundberg (1972), Lynch (1973, 1975a, b, 1978), Moffat (1973), Heyer (1975), Heyer and Liem (1976), Wiley (1976), Hecht and Edwards (1976), Michener (1977), and Enghoff (1981) have relied primarily on outgroup analysis.

In consideration of the asterophryine genera, the most appropriate outgroup is the Genyophryninae, whose status as a group closely related to the Asterophryinae has been established by a synapomorphy, direct development of larvae (Parker 1934).

It is not necessary for the Genyophryninae to be recognized as a distinct taxon in order for it to be an outgroup. Watrous and Wheeler (1981) defined the concept of a functional outgroup and demonstrated that an out-group need not be taxonomically distinct. This concept is similar in application to, though presented more rigorously than, Kluge's (1976) use of the ingroup, *viz.*, that a character state widespread among taxa related at the next higher taxonomic level "that otherwise have little in common" is primitive, a position supported also by Arnold (1981). This is not the same as the "commonality principle" based ingroup analysis, where the more common character state within the group is coded as primitive, a position criticized by a number of workers, including Moffat (1974), Stevens (1980), and Watrous and Wheeler (1981), who demonstrated the logical shortcomings of the

commonality principle. All cladograms based on the commonality principle must root near the middle, and no three-taxon hypothesis can be solved by the commonality principle, since any shared character state must be the more common, hence primitive, and so there can be no shared, derived character states. While it is necessary to demonstrate that the Asterophryinae is a natural group whose monophyly (*sensu* Hennig, 1966) is attested by autapomorphy and that it is therefore possible to postulate its evolution, it is not necessary to the study of the asterophryine genera to establish the naturalness and taxonomic viability of the Genyophryninae.

In the search for evidence of synapomorphy to support the hypotheses of the monophyly of the Asterophryinae and of the Genyophryninae, the outgroup consists of ranoid frogs and microhylids of other subfamilies, listed previously. Myological, skeletal and external morphological data obtained from specimens representing 10 species in the subfamilies Brevicipitinae, Dyscophinae and Microhylinae (Oriental and Neotropical) and 14 ranoid species are used to assess whether either subfamily possesses autapomorphies.

It is considered impossible by many authors to make *a priori* the judgement that the sharing of a given derived character state results from homoplasy; such a judgement can only be made when evidence from different characters is shown to conflict (le Quesne 1969; Cracraft 1981; Wheeler 1981; but Bock, 1981, presents a contrary view). When two characters support incompatible hypotheses of common ancestry, one of them is homoplasious, i.e., the character has been subject to convergence (*sensu lato*) or reversal. Which of the two characters is the homoplasious one remains to be determined.

The approach almost universally advocated, e.g., by Camin and Sokal (1965), Kluge and Farris (1969), Lundberg (1972), Eldredge and Cracraft (1980), Nelson and Platnick (1981), for resolving such conflicts is to favour the cladogram supported by the greatest number of characters, or "the hypothesis that has been rejected the least number of times" (Wiley 1976), and then to reject those characters which do not contribute to the cladogram, on the grounds that they are homoplasies. That is, some form of numerical analysis is suggested in order that the hypothesis of relationships depicted in a cladogram be the most parsimonious, on the grounds that while evolution may not be parsimonious, scientific hypotheses of evolution, as of anything else, must be (Kluge and Farris 1969; Wiley 1975; Cracraft 1979; *contra* Inger, 1967).

However, numerical approaches must be applied to cladistic analyses with caution, as they are based on a number of questionable assumptions (Panchen 1982). First, when one hypothesis of relationships is preferred to another because it is rejected by fewer characters, the notion of what constitutes a character is crucial. A character appears in practice to be any feature of

a group of taxa which is perceived to be relatively constant within taxa but variable between them. It is assumed in using most numerical techniques that all characters used in a cladistic analysis are of equal value to the assessment of relationships. But this need not be the case. For example, characters obtained from different parts of the phenotype may be correlated. Such correlation may be obvious: characters relating to the length of a bone and the site of origin of a muscle on that bone may well be correlated and be treated better as a single character. But correlation may be less obvious. For example, leg length and tongue morphology may well be correlated in a particular case because both may be adaptations to capture of the same kind of food. Hecht and Edwards (1976) showed that radically different interpretations of frog phylogeny resulted from different perceptions of the associations of characters of tadpole morphology. An assessment of character correlation appears to be one of the legitimate roles of functional analysis, which could not be carried out for this study, beyond observations of living specimens during the field trip.

Whether a suite of correlated characters be weighted highly, as suggested by Hecht and Edwards (1976), Hecht (1977), or be given equal weight with other characters is problematical. While the Hecht and Edwards (1976) weighing scheme seems arbitrary, and Hecht's numerical value scheme more so, the principle that some form of assessment of characters to determine their relative "credibility" in the case of conflict (Schlee 1975) seems valid, Moller-Anderson's (1978) caveat regarding the difficulty of applying Schlee's scheme notwithstanding.

A second problem with the use of numerical analyses is the likelihood of high levels of homoplasy in morphologically uniform animals like birds or frogs (Bock 1963; Hecht and Edwards 1976). Such animals are constrained in their evolution by similar developmental possibilities, for example, the physical requirements for flight severely limit the possibilities of evolution of the avian body form. This is particularly so at low taxonomic levels when the animals are genetically similar, and might therefore be expected to evolve independently similar character states under similar environmental constraints. But the history of frog taxonomy gives testimony to a high rate of homoplasy even at family level. Classifications based on features of, for example, the teeth (Günther 1858; Boulenger 1882) and nature of the pectoral girdle (Noble 1931), both characters now believed to have evolved convergently, and incompatible phylogenies of frog families erected by, for example, Hecht (1963) and Inger (1967) on one side and Kluge and Farris (1969) and Lynch (1973) on the other, indicate the high frequency of homoplasy and the difficulty of discerning it even at the family level.

The use of numerical techniques to resolve conflicts between characters presupposes that homologies outnumber homoplasies, or that "evolution is normally

divergent" (Panchen 1982; Friday 1982). This proposition is dubious, for the reasons indicated in the previous paragraph.

One means of resolving these conflicts is to relate observed structures to their functions. Gans (1966) points out that it is not possible to deduce function simply from morphology, and few direct studies of the relation of form and function in living frogs have been carried out, mainly studies of the muscles involved in tongue action, e.g., Gans (1962), Gans and Gorniak (1982) and of the muscles involved in locomotion (Emerson and De Jongh 1980). However, a second approach based on the correlation of morphologies with particular modes of burrowing (Emerson 1976b, Sanders and Davies 1984) has provided dramatic examples of convergence in muscle complexes, as groups of muscles of identical form adapted for similar burrowing techniques are found in frogs from different families.

Other morphological patterns related with particular functions have been identified but not treated. Liem (1970) and Anderson (1978) identify as an adaptation to climbing the division of the *M. palmaris longus* into several slips with separate tendons of insertion, which their comparative studies have shown to be characteristic of treefrogs of several families. Liem based his division of the firmisternal treefrogs (the Rhacophoridae and the Hyperoliidae) into separate families partly on the grounds that the different patterns of division of this muscle indicated that the division had been acquired by different evolutionary steps. That is, it is likely that tree climbing had evolved independently in the two groups. This in turn implies that other derived characters shared by these groups that are recognisable adaptations to tree climbing, e.g., the possession of finger discs and of intercalary cartilages, must be seen as likely convergences.

This is relevant to the asterophryine frogs, all of which spend part of each day underground, and some of which seldom or never emerge above ground, the genera listed in the Introduction as fossorial. Evidence in this group of the adoption of different evolutionary strategies in the adaptation to the fossorial mode may be indirect evidence of convergence in other shared adaptations to the same mode.

Convergence may also be suspected as the source of conflict between apparent synapomorphies in cases where a particular apparently derived morphology is observed to recur in distantly related groups, even if the function is unknown. For example, the reduction of the pectoral girdle in some genera of microhylids and ranids is certainly due to convergence. Possession of a reduced pectoral girdle by different microhylid genera does not seem to be a reliable character in phylogenetic analysis as it has been shown to be liable to convergence, and in cases where this character conflicted with other apparent synapomorphies it would be considered of low value. Panchen (1979, 1982)

indicated a third problem: that the number of synapomorphies detected in a systematic analysis is unlikely to be the complete set of synapomorphies. The assumption must therefore be made in numerical analyses that the ratio of "true" to "false" synapomorphies revealed in the study of a limited number of characters equals the ratio of "true" to "false" synapomorphies in the whole set.

In this study, characters are deemed to be of equal weight unless there is reason to believe that characters are correlated, and then the suite of correlated characters is regarded as equal to one character, on the grounds that such a suite may be deemed to have resulted from but one evolutionary event. In the case of conflicts between characters, judgements as to the relative likelihoods of the relevant character state transformations are made whenever possible. The use of numerical procedures is restricted in this study to the illustration rather than the evaluation of the conflicting hypotheses of relationships in a case where the data conflict intractably.

RESULTS

Taxonomic Recommendations and Nomenclature

In order to avoid confusion and tedious repetition in the following character state analysis, I foreshadow taxonomic recommendations which derive from the analysis, and which I make formally in the systematics section of this paper. Two of the asterophryine genera, *Phrynomantis* and *Xenorhina* (Table 2) are heterogeneous assemblages, and the following changes are necessary. (a) Removal of *Phrynomantis lateralis*, *P. infulata* and *P. louisiadensis* from *Phrynomantis*. These species share a number of character states with *Asterophrys*, *Hylophorbus* and *Pherohapsis* which indicate that it is with those genera that their affinities lie. Their removal from *Phrynomantis* makes this genus a much more natural assemblage supported by autapomorphies. The three species removed from *Phrynomantis* do not fit neatly into any of the other existing genera. I recommend resurrection of *Mantophryne* Boulenger 1897 (type species, *M. lateralis*) to accommodate them, and subsequently refer to these species as *Mantophryne lateralis*, *M. infulata* and *M. louisiadensis*. (b) *Xenorhina doriae* does not conform morphologically with other members of its genus, showing affinities rather to *Phrynomantis (sensu stricto)*, and sharing apomorphies with the other members of that genus. *Xenorhina* becomes a much more uniform group without *X. doriae*, and the remaining members of the reduced genus share many derived characters not shared by *X. doriae*. I recommend that *X. doriae* be transferred to *Phrynomantis* and subsequently refer to it as *Phrynomantis doriae*.

As well as these asterophryine genera, the genyophrynine genus *Cophixalus* is heterogeneous to the extent that it is impossible to make general statements

about it in the following discussions. *Cophixalus darlingtoni* and *C. variegatus* are considered as an entity distinct from *Cophixalus*. As the term *"variegatus*-group" was used by Menzies (1975) to denote a group of four or more small (S-V length approximately 12 mm) cryptic species, I employ the term *"darlingtoni*-group" to refer to the group of species comprising *C. darlingtoni* and the *C. variegatus*-group. Myologically and osteologically, the *darlingtoni*-group is uniform and is clearly more closely related to *Choerophryne* than to other *Cophixalus*, as it shares many unusual characters with *Choerophryne* alone. Whether the *darlingtoni*-group should form a new genus as a sister-group to *Choerophryne* as suggested by Zweifel (*in litt.*, 19 May, 1982) or the definition of *Choerophryne* be broadened slightly to accommodate the *darlingtoni*-group (which may be paraphyletic) is beyond the scope of this study. The removal of the *darlingtoni*-group reduces the heterogeneity of *Cophixalus*. In this study, the term *"Cophixalus"* refers to the genus *Cophixalus*, but excluding the *darlingtoni*-group. As no *Choerophryne* specimens were available for complete dissection, only the superficial musculature of the venter, pectoral girdle and throat and the jaw musculature were examined in this genus and details of the osteology were derived from Menzies and Tyler (1977).
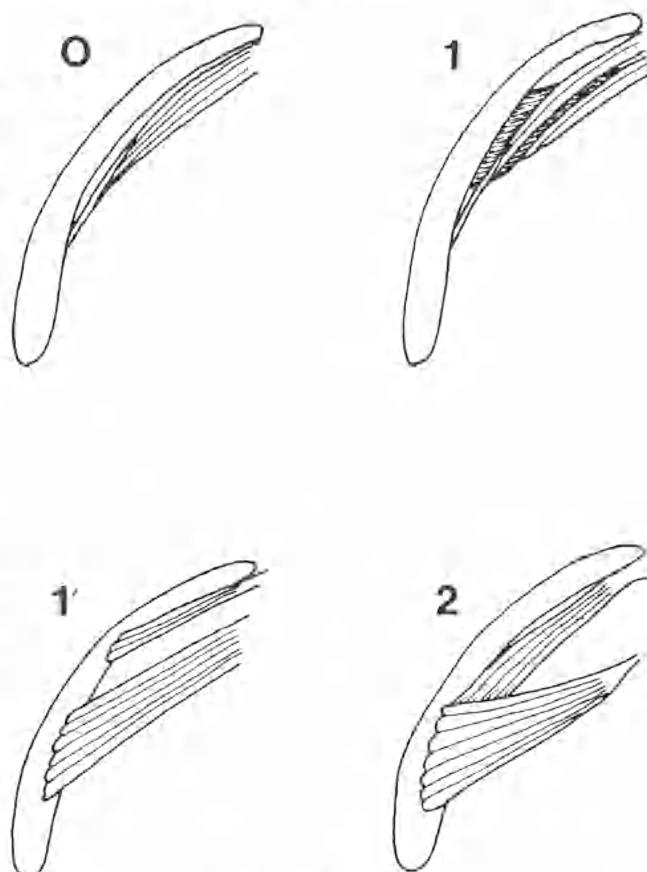

FIG. 4. Supplementary slips to the *M. intermandibularis* in asterophryines. *Abbreviations:* 0, State (0) single origin via a tendon; 1, State (1) origins via a tendon and direct from the dentary; 1', State (1') origins from the ventral surface of the angulosplenial; 2, State (2) origins from adjacent parts of the ventral surface of the angulosplenial.
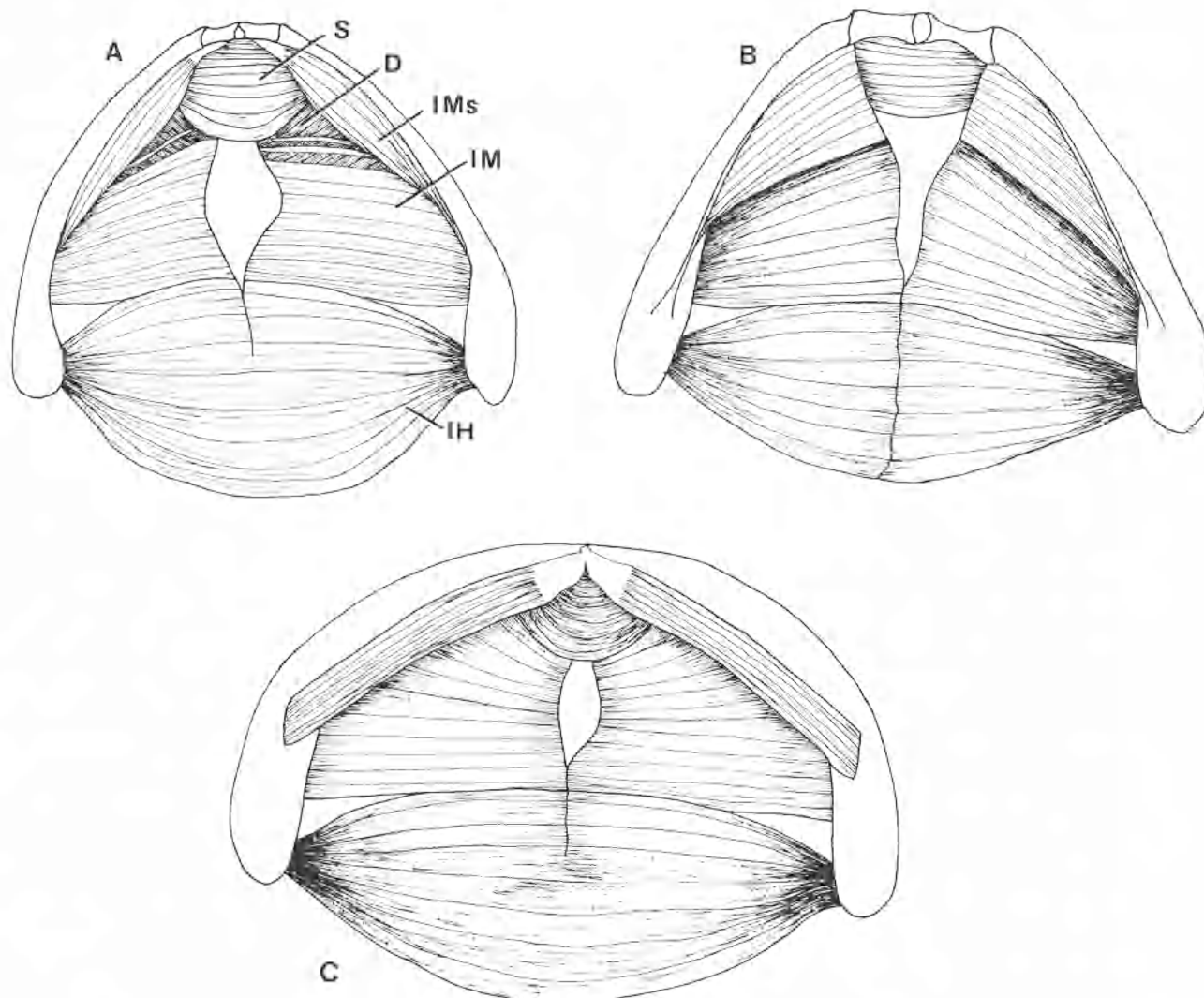
FIG. 5 Superficial mandibular musculature of (A) *Cophixalus kaindiensis* AUZ; (B) *Copiula fistulans* AUZ D742; (C) *Genyophryne thomsoni* UPNG 5130. Abbreviations: D, dorsal slip of the *M. interhyoideus*; IH, *M. interhyoideus*; IM, *M. intermandibularis*; IMs, supplementary slip of *M. intermandibularis*; S, *M. submentalis*.

Character State Analysis

The characters discussed are ones which vary in such a way as to be of potential use in a phylogenetic study of the asterophryines or to shed light on relationships between the Asterophryinae and Genyophryninae. Characters which are numbered are those whose states are distributed in such a way as to warrant subsequent discussion. The distribution of the states of these characters are listed in Table 4. States designated 0 are primitive states. States designated 1, 1', 1'' etc. are derived, but the relationship between these derived states is unknown. States designated 1, 2, 3, etc. are derived with the polarity 1 → 2 → 3 etc. States designated by letters are states of unknown polarity, i.e., the primitive state cannot be identified.

The *M. submentalis*: Variation in the attachments of this muscle is in part related to the shape of the mentomeckelians. In the Asterophryinae alone the mentomeckelians are posterior to the dentaries and deflected posteroventrally. Consequently, the mentomeckelians are more prominent sites of attachment of the *M. submentalis* in asterophryines

than in other microhylids, and in at least some species of *Xenorhina* the mentomeckelians are the only site of attachment. I treat this involvement of the mentomeckelians in asterophryines as a character of the mentomeckelians, below.

Among the asterophryines there is wide variation in the posterior extent of the *M. submentalis* reaching an extreme expansion in *Barygenys atra* (Fig. 6), but this variation is partly independent of generic classifications and so cannot be employed in a phylogenetic analysis at the generic level.

Character 1. Nature of the supplementary slips of the *M. intermandibularis.* Four states occur among the asterophryines (Fig. 4): (0) a single supplementary slip arising via a tendon (*Hylophorbus, Pherohapsis* and *Mantophryne*); (1) two supplementary slips, the anterior arising via a tendon, the posterior direct from the dentary (*Phrynomantis*) (Burton, 1983): (1') two supplementary strap-like slips from the ventral surface of the angulosplenial, the posterior slip inserting on the median aponeurosis of the *M. intermandibularis* (*Asterophrys, Xenobatrachus* and *Xenorhina*) (Fig. 6);
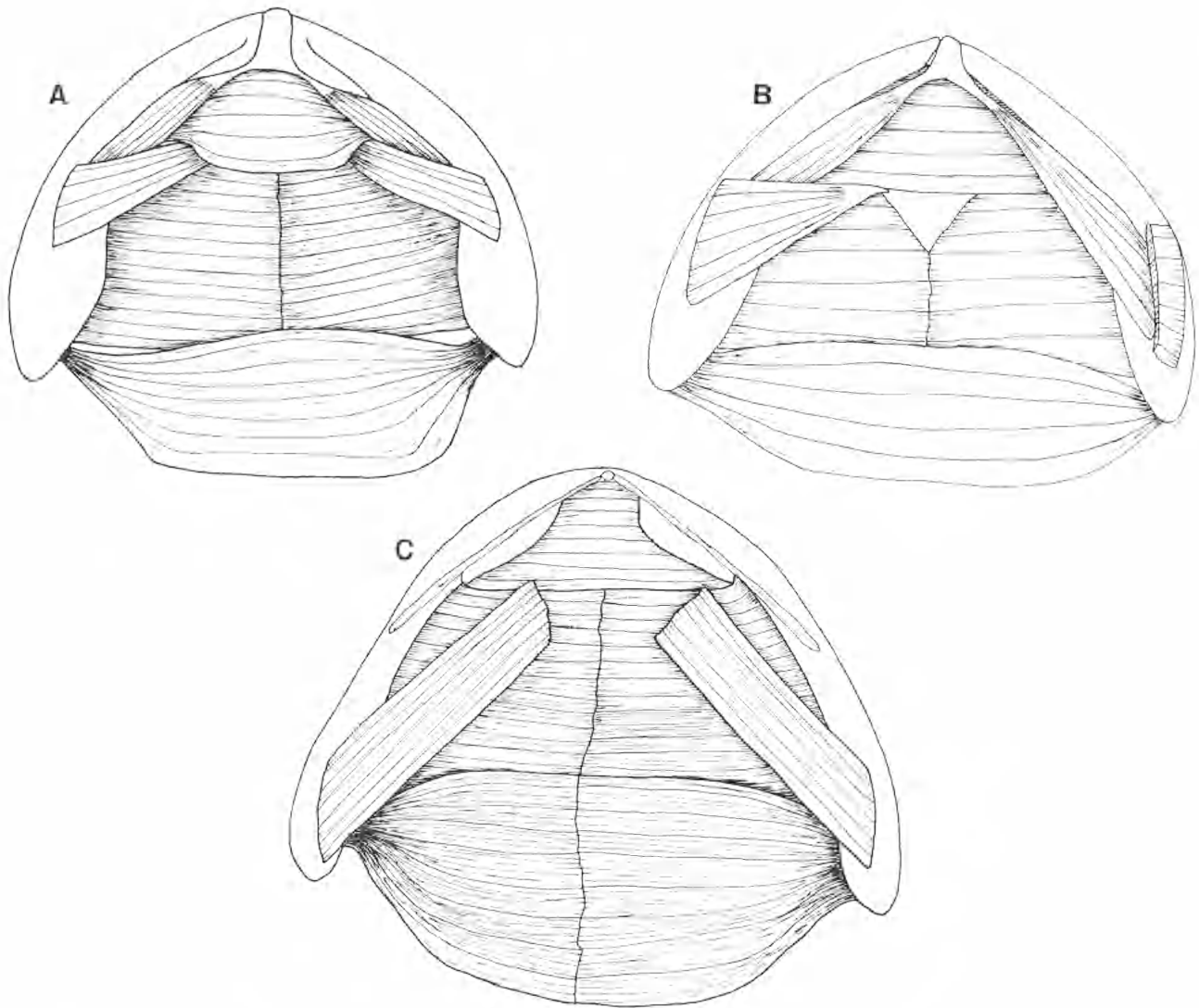
FIG. 6. Superficial mandibular musculature of (A) *Barygenys flavigularis* AUZ D741; (B) *Barygenys atra* UPNG 3836, left posterior supplementary slip removed; (C) *Xenobatrachus rostratus* SAMA R9386a.

and (2') two supplementary slips from the angulosplenial, the posterior slip inserting via a narrow tendon on the *M. genioglossus basalis* (*Barygenys*) (Fig. 6).

State (0) occurs also in the Genyophryninae (Burton, 1984), and is primitive among the Asterophryinae. State (1) is likely to have evolved directly from State (0), and State (2') may have evolved from State (1'), but it is not clear whether State (1') evolved from State (1) or directly from State (0). The polarities are either 0 → 1 → 1' → 2' or 2' ← 1' ← 0 → 1.

Character 2. Occurrence of a dorsal sheet of posteromedially directed fibres on the *M. intermandibularis.* Two states occur among the Papuan microhylids: (0) dorsal fibres present (Genyophryninae) (Burton 1984, Fig. 5A). These fibres are not always visible from the ventral surface (Figs 5B, 5C); and (1) dorsal fibres absent (Asterophryinae).

State (0) is shared by the other microhylids examined, and is primitive among the Papuan microhylids.

Character 3. Overlap of the *Mm. intermandibularis* and *interhyoideus.* Two states occur among the Papuan microhylids: (0) no overlap (Genyophryninae (Burton 1984, Fig. 5), except *Cophixalus pansus* and *C. riparius; Xenorhina bouwensi*); and (1) overlap of the muscles, the anterior fibre of the *M. interhyoideus* lying on the ventral surface of the posterior fibres of the *M. intermandibularis* (Asterophryinae (Burton 1983, Fig. 6) except *Xenorhina bouwensi;* also *Cophixalus pansus* and *C. riparius*).

State (0) is shared by most of the other microhylids examined, and is primitive. Overlap occurs also in *Calluella* and *Kaloula,* but it is different in form from State (1) as it is the *M. intermandibularis* which overlaps on the ventral surface of the *M. interhyoideus* in these two genera. The possession of State (0) by Papuan microhylids appears to be related to small size. *Xenorhina bouwensi* (17.9, 21.3, 20.7 mm S-V) is the smallest asterophryine examined, while *Cophixalus riparius* is the largest genyophrynine examined, and *C. pansus* among the most densely muscled. Similarly,
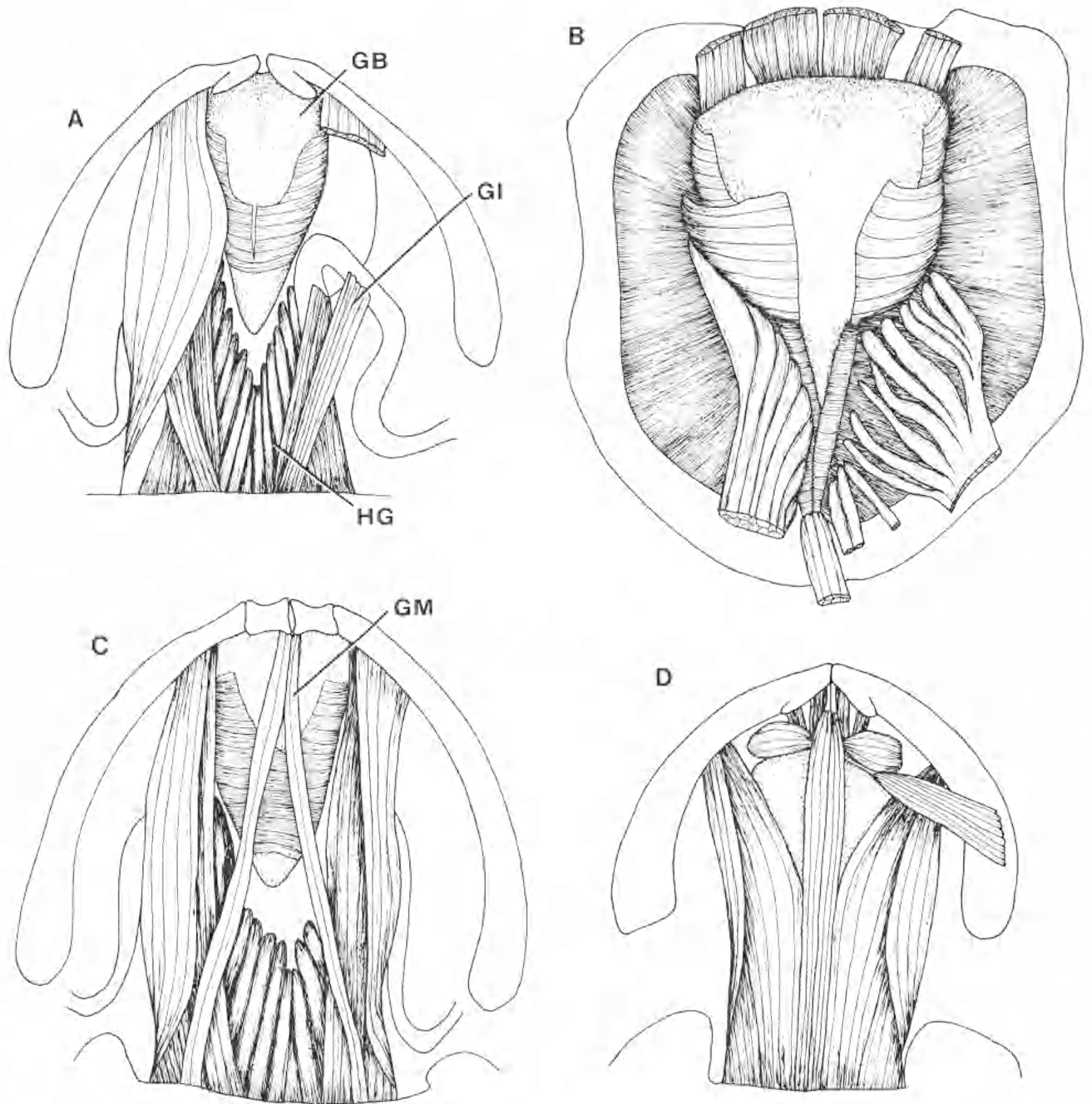
FIG. 7. (A) Deeper musculature of the throat of *Hylophorbus r. rufescens* AUZ D738, left *M. geniohyoideus lateralis externus* severed to reveal the *M.g.l. internus* origin from the hyale; (B) Tongue musculature of *Xenobatrachus giganteus* UPNG 5680; (C) Deeper throat musculature of *Sphenophryne schlaginhaufeni* AUZ B733; (D) *Barygenys flavigularis* AUZ D741, the left posterior supplementary slip to the *M. intermandibularis* not removed. Abbreviations: GB, *M. genioglossus basalis*; GI, *M. geniohyoideus lateralis internus*; GM, *M. genyohyoideus medialis*; HG, *M. hyoglossus*.

Calluella and *Kaloula* are the largest of the other microhylids examined.

Character 4. Occurrence of the *M. geniohyoideus medialis*. Two states occur in the asterophryines: (0) *M.g. medialis* present (*Barygenys*) (Fig. 7C), (1) *M.g. medialis* absent (other asterophryines (Fig. 7A, B)).

State (0) is shared by all genyophrynines, and is the primitive state for the asterophryines.

Character 5. Origin of the *M. geniohyoideus lateralis internus*. Three states occur in the asterophryines: (A) origins from the dentary and the hyale (*Phrynomantis*) (Burton 1983); (B) origin from the dentary only

(*Barygenys* (Fig. 7C), *Xenobatrachus* and *Xenorhina*); and (C) origin from the hyale only (*Asterophrys*, *Hylophorbus* (Fig. 7A), *Mantophryne* and *Pherohapsis*).

All of these states occur among the genyophrynines and so polarities cannot be assigned by out-group analysis.

Character 6. The *M. genioglossus*. Three states occur among the Asterophryinae: (0) the *M.g. basalis* labiform, and the *M.g. dorsalis* comprising two strap-like muscles (*Asterophrys*, *Hylophorbus*, *Mantophryne*, *Pherohapsis* and *Phrynomantis*) (Fig.
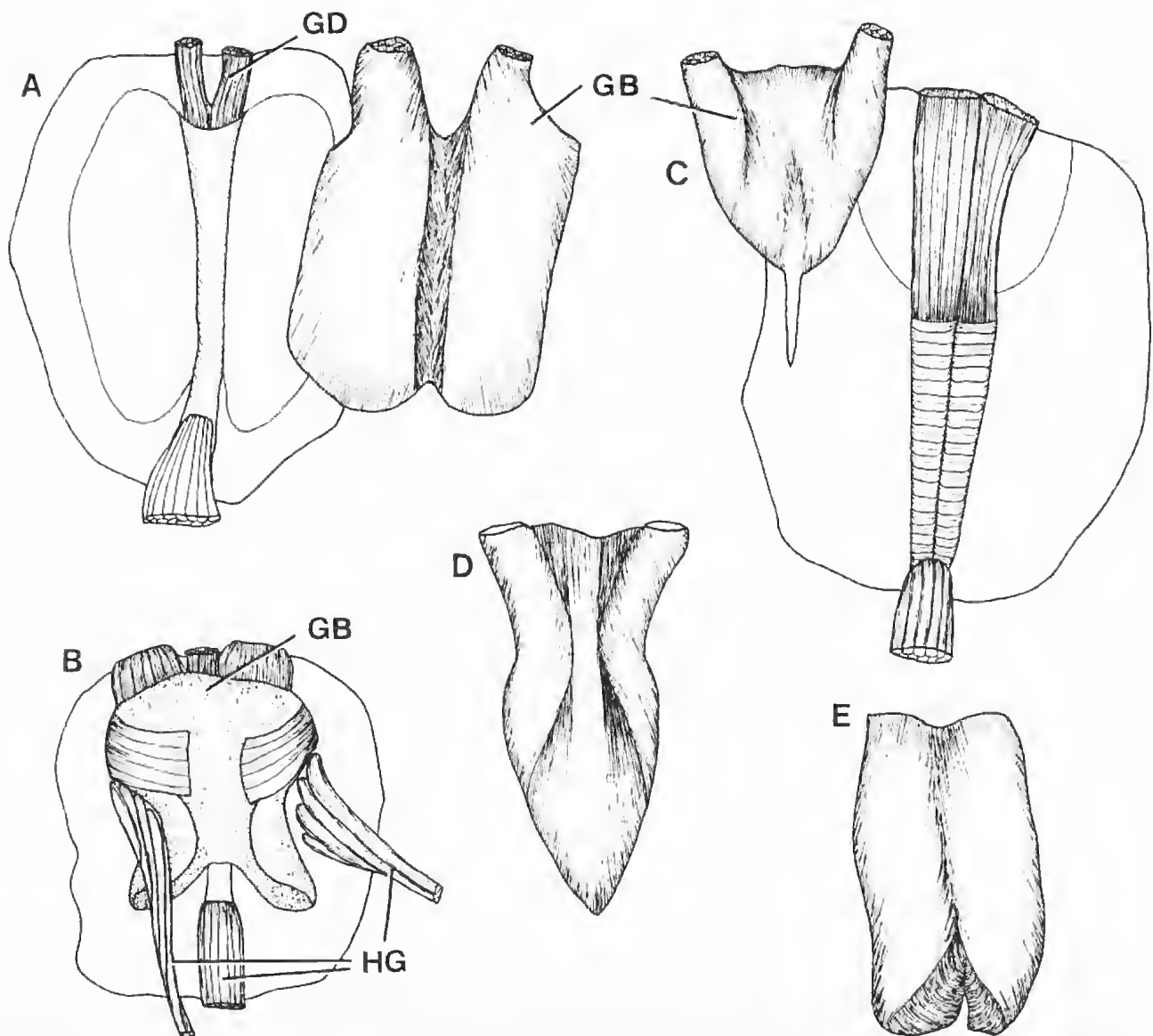
FIG. 8. (A) Ventral view of the *M. genioglossus* of *Barygenys atra* UPNG 3836, *M.g. basalis* reflected to the left to reveal *M.g. dorsalis*; (B) Ventral view of the deepest muscles of the tongue of *Barygenys flavigularis* AUZ D741; (C) Ventral view of the *M. genioglossus* of *Xenobatrachus giganteus* UPNG 5680, *M.g. basalis* reflected to the right to reveal *M.g. dorsalis*; (D) Dorsal view of the *M.g. basalis* of *Phrynomantis stictogaster* SAMA R20886; (E) Dorsal view of the *M.g. basalis* of *Genyophryne thomsoni* UPNG 5130. Abbreviations: GB, *M. genioglossus basalis*; GD, *M.g. dorsalis*; HG, *M. hyoglossus*.

7A); (1) the *M.g. basalis* bearing a posterad cultriform process, and the *M.g. dorsalis* comprising two strap-like muscles (*Xenobatrachus* and *Xenorhina*) (Figs 7B, 8C); and (1') the *M.g. basalis* lamellate and folded, and the *M.g. dorsalis* fused and ensheathed in connective tissue (*Barygenys*) (Figs 8A, 8B).

State (0) is the usual state among microhylids including all genyophrynines except the unique *Genyophryne*, and is the primitive state. In *Genyophryne* (Fig. 8D) the *M. genioglossus* is short and bilobular and unlike that of any other microhylid examined. There is no evidence to indicate the relationship between states 1 and 1'.

Character 7. Occurrence of a deep slip of the *M. hyoglossus*. Two states occur in the Papuan microhylids: (0) slip present (Genyophryninae, except

Genyophryne); and (1) slip absent (Asterophryinae and *Genyophryne*).

State (0) appears to be the usual microhylid condition (Trewavas 1933), and is probably the primitive state of the Papuan microhylids. Its absence in *Kaloula* is interpreted as a case of parallel evolution.

Barygenys possesses a unique state of the *M. hyoglossus* (Fig. 8A), but the reduction and division of this muscle into three narrow, discrete sections appears to have evolved in association with the lamellate *M. genioglossus basalis*, which excludes the *M. hyoglossus* from access to the tongue except at three sites: the two lateral folds of the *M.g. basalis* and the posterior notch in the *M.g. basalis*. As the forms of these two muscles are so intimately related, they cannot be considered separately.
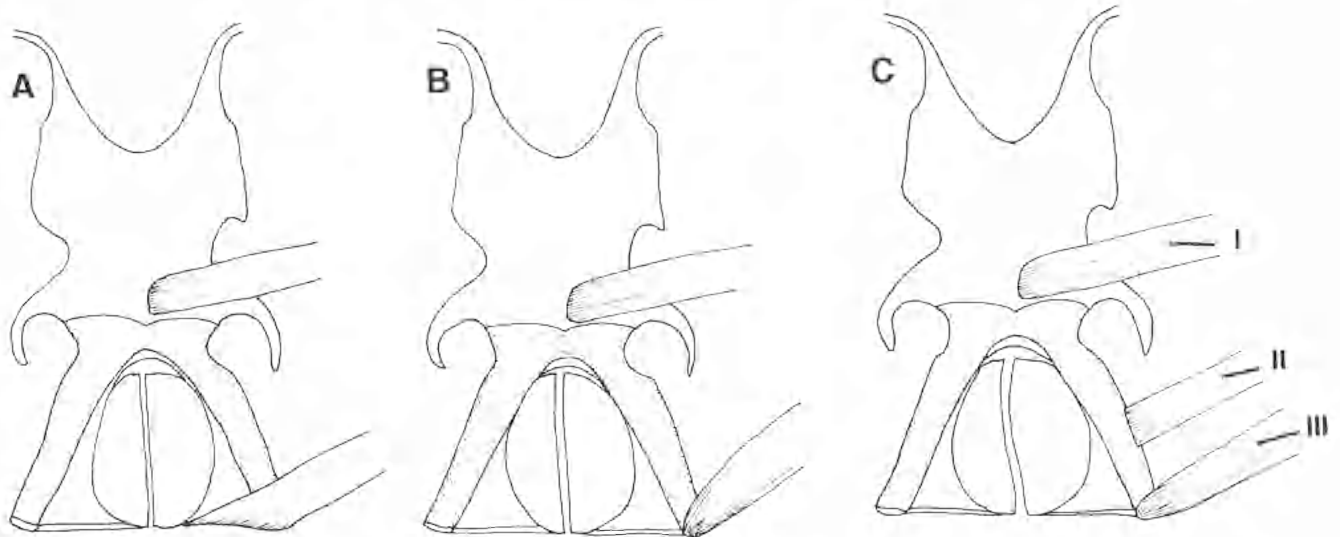
FIG. 9. Insertions of the *Mm. petrohyoidei posteriores* in Papuan microhylids. (A) State (0) two *Mm. p. posteriores*, the posterior of which inserts on the tip of the postero-medial process of the hyoid and the hyocricoid ligament; (B) State (1) two *Mm. p. posteriores*, the posterior of which inserts only on the tip of the posteromedial process of the hyoid; (C) State (1') three *Mm. p. posteriores*. Abbreviations: I, *M. petrohyoideus posterior* I; II, *M.p. posterior* II; III, *M.p. posterior* III.

Character 8. Number and insertions of the *Mm. petrohyoidei posteriores*. Three states occur among the Papuan microhylids (Fig. 9): (0) two *Mm. p. posteriores*, the posterior of which inserts on the epicondyle of the posteromedial process of the hyoid and the adjacent hyocricoid ligament (Genyophryninae, except *Genyophryne*) (Fig. 10A); (1) two *Mm. p. posteriores*, the posterior of which inserts on the epicondyle alone (*Barygenys*) (Fig. 10B); and (1') three *Mm. p. posteriores*, of which the *M.p. posterior* II inserts on the hyocricoid ligament, and the *M.p.*
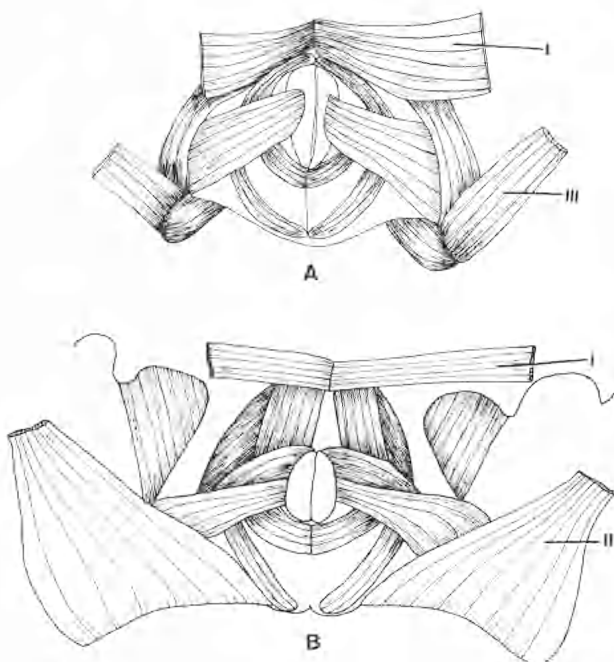

FIG. 10. Dorsal view of the larynx of (A) *Cophixalus riparius* SAMA R5216a; (B) *Barygenys atra* UPNG 3836. Abbreviations: I, *M. petrohyoideus posterior* I; III, *M.p. posterior* III.

posterior III on the epicondyle (Asterophryinae except *Barygenys; Genyophryne*) (Burton 1983).

State (0) is shared by *Calluella*, the Oriental microhylines and *Gastrophryne* (Trewavas 1933) and is primitive among the Papuan microhylids. The occurrence of State (1') in *Elachistocleis* is interpreted as a case of convergence. While State (1') appears to have derived directly from State (0) by division of the muscle, it is unclear whether State (1) derives from State (0) or from State (1').

Character 9. Two states of the origin of the *M.p. posterior* III occur in the Asterophryinae: (0) origin from the otic ramus of the squamosal and the adjacent exoccipital (*Barygenys, Xenobatrachus* and *Xenorhina*) (Fig. 11C), and (1) origin from the zygomatic ramus of the squamosal (*Hylophorbus, Phrynomantis, Mantophryne infulata* and *M. louisiadensis*) or its posterad projection (*Asterophrys, Pherohapsis* and *Mantophryne lateralis*) (Figs 11A, B).

State (0) is shared by the genyophrynines (Fig. 11D) and is primitive among the asterophryines.

Character 10. Extent of the anterior origin of the *M. depressor mandibulae*. Two states occur among the asterophryines: (0) origin from the entire ventral margin of the tympanic ring, and in some small specimens also from the adjacent epimysium of the *M. adductor mandibulae externus superficialis* (*Phrynomantis*, except *P. doriae*) (Fig. 11A); and (1) from the posterior 1/2 only of the ventral margin (*Asterophrys, Barygenys, Hylophorbus, Pherohapsis, Xenobatrachus, Xenorhina, Phrynomantis doriae* and *Mantophryne*) (Fig. 11C).

State (0) is shared by the genyophrynines (Fig. 11D), and is primitive.

Character 11. Extent of the slip of the *M. depressor mandibulae* from the otic ramus. Two states occur
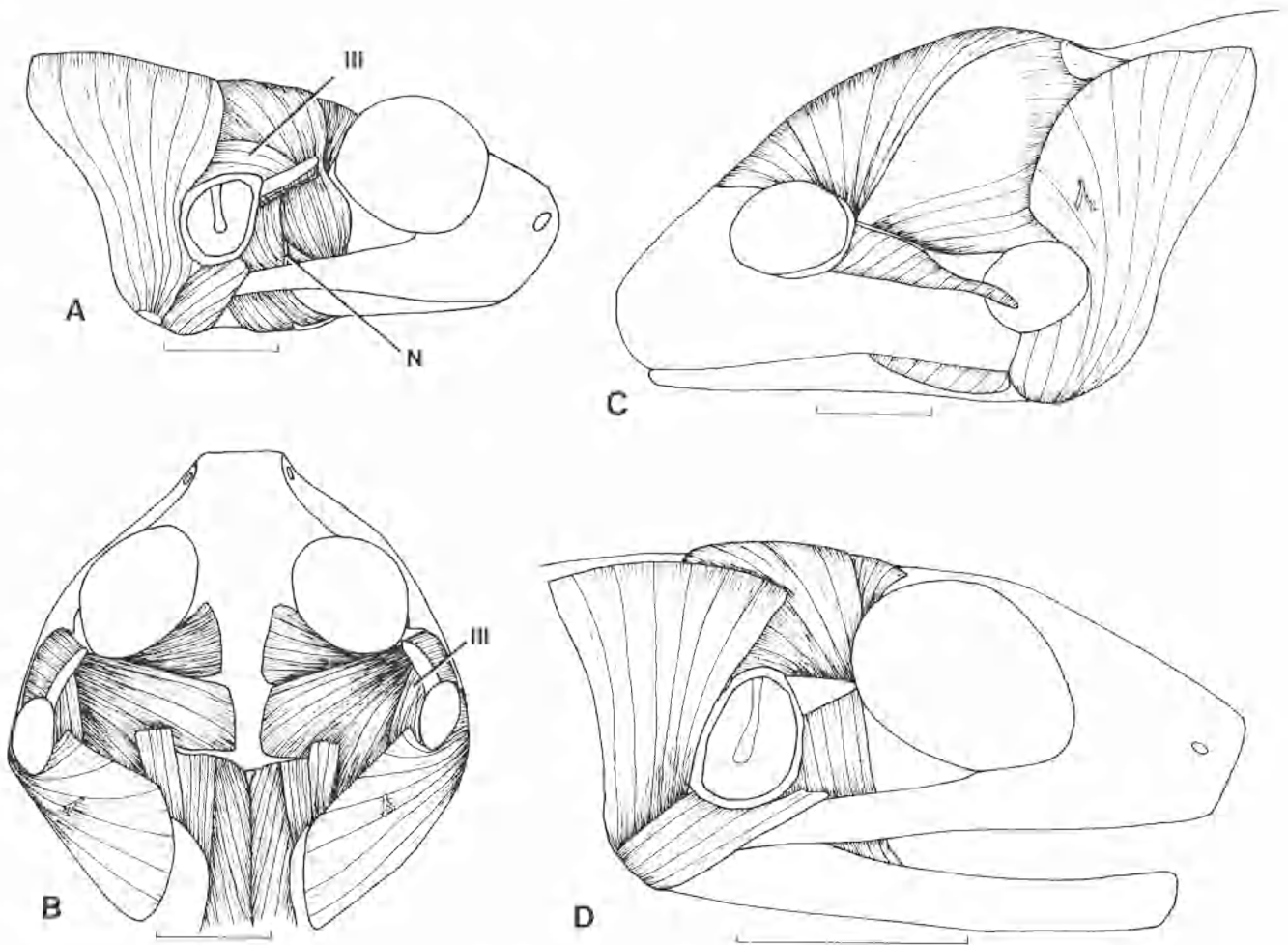
FIG. 11. A. Right lateral view of the jaw musculature of *Phrynomantis h. humicola* MCZ 52970, *M. adductor mandibulae externus superficialis* removed to reveal the position of the mandibular branch of the trigeminal nerve; B. Dorsal view of the jaw musculature of *Phrynomantis wilhelmana* AM R66747; C. Left lateral view of the jaw musculature of *Xenobatrachus giganteus* UPNG 5680; D. Right lateral view of jaw muscles of *Sphenophryne schlaginhaufeni* AUZ B733. Scale bar = 5 mm. Abbreviations: N, trigeminal nerve; III, origin of *M. petrohyoideus posterior*.

among the asterophryines: (0) origin relatively small, significantly less bulky than the slip from the dorsal fascia, or absent (*Asterophrys, Barygenys, Hylophorbus, Mantophryne, Pherohapsis* and *Phrynomantis*); and (1) origin relatively extensive, approximately equal in bulk to the slip from the dorsal fascia (*Xenobatrachus, Xenorhina*).

State (0) is shared by all genyophrynines, except *Choerophryne* and the *darlingtoni*-group, which share an unusual conformation of the depressor musculature, which does not occur in asterophryines. State (0) is considered primitive among the asterophryines.

Character 12. Development of the *M. adductor mandibulae posterior longus*. Three states occur among the asterophryines: (0) the fibres passing directly from their origins on the surfaces of the frontoparietal, prootic and exoccipital to a tendon placed anterolaterally in the orbit, the fibres not organized into discrete segments (*Hylophorbus, Mantophryne, Pherohapsis* and *Phrynomantis*) (Figs 11B, 12A); (1) the fibres from the frontoparietal passing laterally and the fibres from the prootic and exoccipital passing anteriorly, so that the two sets of fibres form segments (*Asterophrys*);

and (2) the fibres organized into segments as in State (1), some fibres from the more posterior origin inserting on a superficial tendon which unites distally with the usual deep tendon of insertion (*Barygenys, Xenobatrachus* and *Xenorhina*) (Fig. 11C).

State (0) is shared by the genyophrynines (Fig. 11D) and is primitive. States (1) and (2) appear to be by-products of the massiveness of the adductor muscles of *Asterophrys, Barygenys, Xenobatrachus* and *Xenorhina*. The direction of evolution 1 → 2 is associated in part with a diminution of the relative size of the skull, and a consequent tendency of the jaw muscles to bulge in *Barygenys, Xenobatrachus* and *Xenorhina*.

The exclusion of the *M.a.m. posterior longus* from an exostosed or otherwise adorned skull in *Asterophrys, Hylophorbus, Mantophryne* and *Pherohapsis* is considered below as a character state of the skull.

Character 13. Origin of the *M. adductor mandibulae externus superficialis*. Two states occur among the asterophryines: (0) origin from the zygomatic ramus of the squamosal, with little or no origin from the fascia between the anterior tip of the zygomatic ramus
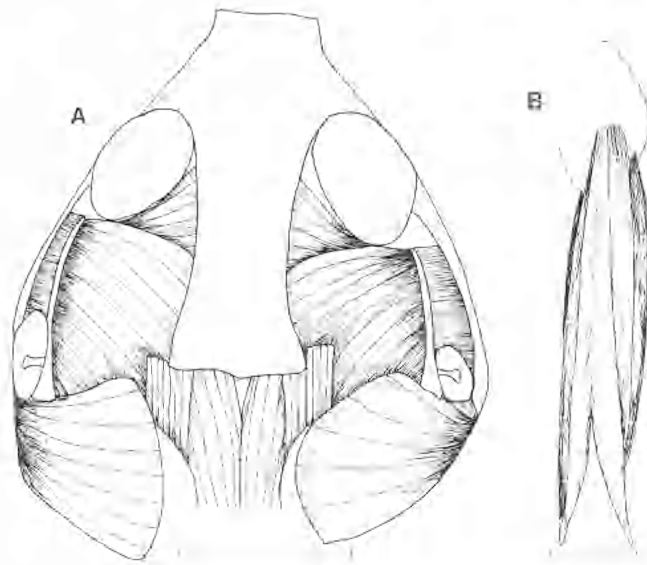
FIG. 12. A. Dorsal view of the jaw musculature of *Mantophryne lateralis* AUZ D737; B. Anterior muscles of the shank of *Mantophryne lateralis* AUZ D737. Scale bar = 5 mm.

and the eye (*Asterophrys, Hylophorbus, Pherohapsis, Mantophryne* and *Phrynomantis*) (Figs 11A, B, 12A); and (1) an extensive origin from the fascia anterior to the anterior tip of the zygomatic ramus (*Barygenys, Xenobatrachus* and *Xenorhina*) (Fig. 11C).

State (0) is shared by the genyophrynines (Fig. 11D) and is primitive. State (1) is related to the long expanse between the tip of the zygomatic ramus and the eye in *Barygenys, Xenobatrachus* and *Xenorhina*, which in turn is related to the smallness of the eye in these two genera, and consequently this character cannot be considered independently of Character 47: eye-size.

The origin of this muscle in *Pherohapsis* is modified as a result of the connexion between the zygomatic ramus and the maxilla, but although the *M.a.m. externus superficialis* is entirely deep to this sheet of bone, its origin is from the zygomatic ramus as in other asterophryines.

The Trigeminal nerve: The position of the mandibular branch of the trigeminal nerve is too inconsistent to be useful as a character in phylogenetic analysis.

Character 14. Insertion of the *M. longissimus dorsi.* Two states occur among the asterophryines: (0) insertion on the exoccipital (Asterophryinae except *Barygenys*) (Figs 11B, 12A); and (1) insertion partly on the dorsal fascia (*Barygenys*).

State (0) is shared by genyophrynines, and is primitive among the asterophryines.

The *M. ileolumbaris:* Two states of the *M. ileolumbaris* occur among the asterophryines: origin from the tip of the iliac shaft (*Asterophrys, Barygenys, Phrynomantis, Xenobatrachus, Xenorhina* and *Mantophryne louisiadensis*); and origin from a site well posterior to the tip (*Hylophorbus, Pherohapsis, Mantophryne infulata* and *M. lateralis*). Both states occur in the genyophrynines. The former state occurs

in species with the ilio-sacral articulation type IIA of Emerson (1979), and the latter in species with a type I articulation. This character cannot be considered independently of Character 46: "ilio-sacral articulation type".

Character 15. Tendinous inscriptions in the *M. rectus abdominis.* Two states occur among the microhylids: (A) one abdominal tendinous inscription (Asterophryinae, Genyophryninae and *Breviceps*); and (B) three abdominal tendinous inscriptions (*Microhylinae* and *Calluella*).

Neither state occurs among the ranoids in which two states occur: four abdominal tendinous inscriptions (most genera); and two abdominal tendinous inscriptions (*Hemisus*). It is impossible from such data to determine the primitive state in the microhylids.

Character 16. Extent of fibres of the *Mm. obliqui abdominis externus* and *transversus abdominis.* Two states occur among the asterophryines: (0) ventral insertions on a broad tendon which covers the ventral abdomen (*Asterophryinae,* except *Barygenys;* and (1) fibres from the two sides meeting on the mid-ventral surface of the abdomen, at least in part (*Barygenys*)).

State (0) is shared by the genyophrynines and is primitive among the asterophryines.

The origin of the *M. rhomboideus anterior.* Two states occur among the asterophryines: origin entirely from the exoccipital (*Asterophrys, Pherohapsis*); and origin partly from the dorsal fascia (*Barygenys, Hylophorbus, Mantophryne, Phrynomantis, Xenobatrachus* and *Xenorhina*) (Figs 11B, C, 12A).

Both states occur among the genyophrynines. The condition of this muscle in *Asterophrys* and *Pherohapsis* could be related to modifications of the skulls of these genera. The genyophrynines which possess a partial orgin from the dorsal fascia are the more heavily muscled terrestrial or fossorial species (*Cophixalus neglectus, C. pansus, Copiula, Genyophryne* and *Sphenophryne*), and this condition may be related to the utilization of an additional site of origin in the face of crowding by muscles of the limited skull surface. This character will not be considered further.

Character 17. Insertion of the *M. serratus medius.* Two states occur among the asterophryines: (0) two insertions on the suprascapula: one dorsal and one ventral to the site of insertion of the *M. levator scapulae superior* (*Asterophryinae,* except *Barygenys*); and (2) one insertion posterior to the insertions of the *Mm. levatores (Barygenys).*

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 18. Origins of the *M. levator scapulae inferior.* Two states occur among the asterophryines: (0) origin partly from the ventral surfaces of the two anterior vertebrae (*Asterophrys, Hylophorbus, Mantophryne, Pherohapsis* and *Phrynomantis*) (Burton 1983); and (1) origin partly from the ventral
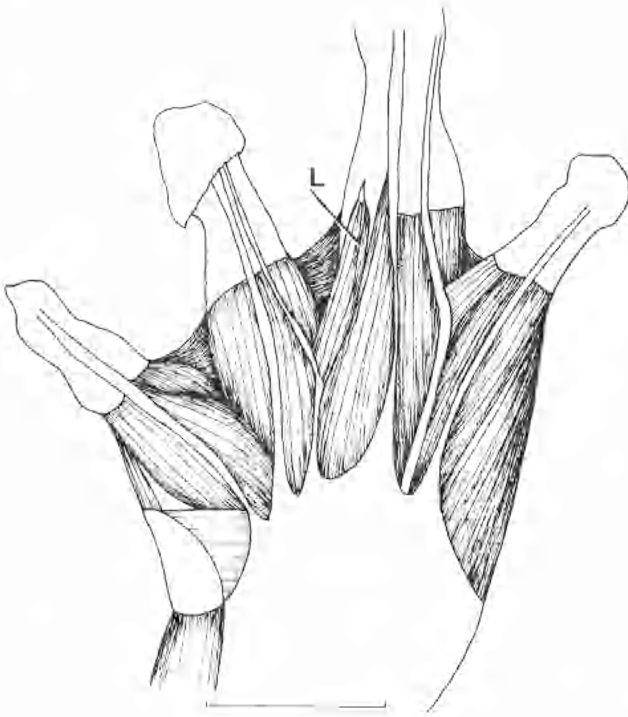
FIG. 13. Ventral superficial muscles of right manus of *Barygenys ulra* UPNG 3836. Abbreviation: L, *M. lumbricalis brevis digiti* IV. Scale bar = 1 mm.

surfaces of the three anterior vertebrae (*Barygenys, Xenobatrachus* and *Xenorhina*).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 19. Development of a deep slip of the *M. pectoralis sternalis.* Two states occur among the asterophryines: (0) deep slip poorly developed and uniting distally with the superficial muscle (*Asterophrys, Hylophorbus, Mantophryne, Pherohapsis* and *Phrynomantis*); and (1) deep slip well-developed, oblique to the superficial muscle and inserting separately (*Barygenys, Xenobatrachus* and *Xenorhina*).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 20. Origin of the *M. lumbricalis brevis digiti* IV of the manus. Two states of the origin of the medial slip occur among the asterophryines: (0) origin from a superficial tendon, muscle slender (*Barygenys*) (Fig. 13); and (1) origin via a short, stout tendon from the centrale postaxiale; muscle large and fusiform (*Asterophryinae,* except *Barygenys*) (Burton 1983).

State (0) occurs in *Cophixalus riparius* and *Genyophryne thomsoni* among the genyophrynines. In all genyophrynines this is a slender muscle arising from a long narrow tendon, usually from the palmar aponeurosis. State (1) does not occur among the genyophrynines. State (0) is considered primitive among the asterophryines.

Character 21. Position of division of the *M. tibialis anticus longus* into bellies. Two states occur among the asterophryines: (A) within the proximal 2/3 of the

muscle (*Barygenys, Pherohapsis, Phrynomantis, Xenobatrachus* and *Xenorhina*) (Burton 1983); and (B) division within the distal 1/4 of the muscle (*Asterophrys, Hylophorbus* and *Mantophryne*) (Fig. 12B).

As both states occur among the genyophrynines, no polarities can be ascribed to the states of this character, which may well be correlated with Character 22.

Character 22. Origin of the *M. tibialis anticus brevis.* Two states occur among the asterophryines: (0) origin entirely or partly within the proximal 2/3 of the tibiofibula (*Barygenys, Phrynomantis, Xenobatrachus* and *Xenorhina*); and (1) origin entirely within the distal 1/4 of the tibiofibula (*Asterophrys, Hylophorbus, Mantophryne* and *Pherohapsis*).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 23. Origin of the *M. opponens hallucis.* Two states occur among the asterophryines: (0) origin from the tarsalia (*Asterophryinae,* except *Barygenys*) (Burton 1983); and (1) origin from the dorsal surface of the plantar aponeurosis (*Barygenys*).

State (0) is shared by the genyophrynines, and is primitive.

Character 24. Union of the *Mm. lumbricales breves digitorum* IV and V. Two states relating to the degree of fusion of the lateral slip of the *M.l.b. digiti* IV and the medial slip of the *M.l.b. digiti* V occur in the asterophryines: (0) separation proximal, much less than 1/2 the medial slip of the *M.l.b. digiti* V involved in fusion (*Barygenys*); and (1) separation distal, the *M.l.b. digiti* V almost entirely fused to the *M.l.b. digiti* IV (*Asterophryinae,* except *Barygenys*).

State (0) is shared by the Genyophryninae, and is primitive among the asterophryines.

Character 25. Relative breadth of the frontoparietals. Two states occur among the asterophryines: (0) frontoparietals broad, length approximately 2× breadth of the combined frontoparietals (*Barygenys*) (Fig. 14A); and (1) frontoparietals relatively narrow, length approximately 3× the breadth (*Asterophryinae,* except *Barygenys*) (Figs 14C, 15A, C, E, 16A, C).

State (0) is shared by the genyophrynines (Figs 17A, 18A) and is primitive among the asterophryines.

Character 26. Occurrence of parasagittal ridges on the frontoparietals. Two states occur among the Papuan microhylids: (0) parasagittal ridges lacking (*Barygenys, Phrynomantis, Xenobatrachus, Xenorhina* and *Genyophryninae* except *Genyophryne*) (Figs 14A, C, 15A, 18A); and (1) parasagittal ridges present (*Hylophorbus, Mantophryne, Pherohapsis* and *Genyophryne*) (Fig. 16C).

State (0) occurs in the other microhylids and is primitive in the Papuan microhylids. The frontoparietals differ in form among those microhylids exhibiting State (1). In Hylophorbus *and* Mantophryne infulata *the ridges are small, and the area between the ridges is unadorned. In the other taxa the area between the ridges is rugose, and the effect is that the mid-dorsal*
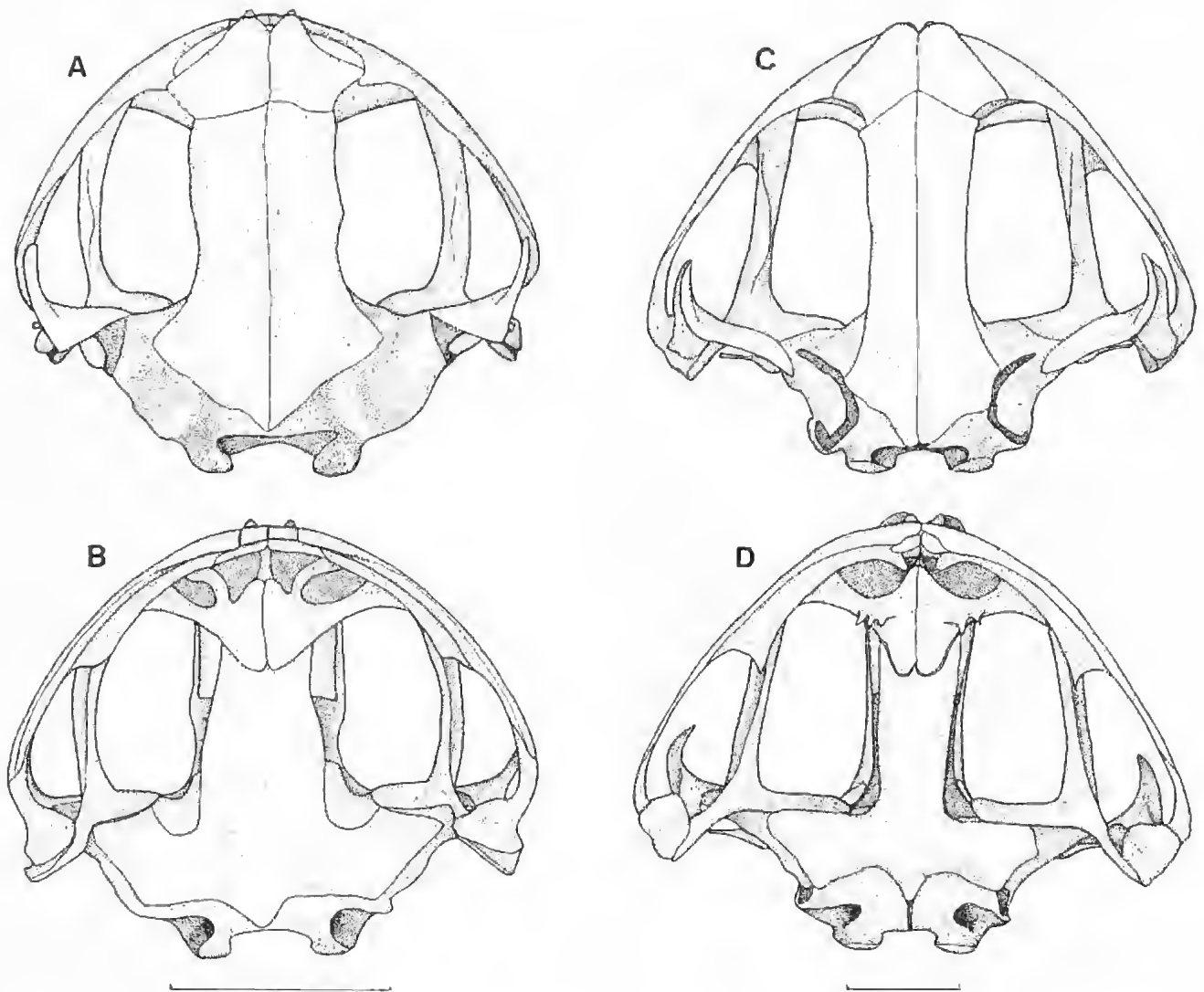
FIG. 14. A. Dorsal and B. ventral view of the skull of *Barygenys atra* UPNG 3836; C. Dorsal and D. ventral views of the skull of *Xenobatrachus giganteus* UPNG 5680. Scale bar = 5 mm.

surface of the cranium appears as a rugose plateau. It is assumed that the two conditions described are alternative forms of the one state. The state of *Asterophrys* (Fig. 16A) is not clear (see discussion of Character 27, following).

Character 27. Occurrence of a sagittal crest on the cranium. Two states occur among the asterophryines: (0) sagittal crest lacking (Asterophryinae except *Asterophrys* and some specimens of *Xenobatrachus obesus* and *Phrynomantis doriae*); and (1) sagittal crest present (*Asterophrys* and some specimens of *Xenobatrachus obesus* and *Phrynomantis doriae*) (Figs 15C, 16A).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines. The development of a strong sagittal crest in large specimens of *Phrynomantis doriae* and *Xenobatrachus obesus* clearly results from an ontogenetic effect — progressive lateral compression of the frontoparietals and raising of a sagittal crest as the frontoparietals are forced against each other. This may result from the disproportionate development of adductor muscles during ontogeny. The crest of the small specimen of *Asterophrys* that I examined was very similar to that of the largest specimen of *P. doriae*, but the specimen figured by Zweifel (1972) possesses an exostosed plateau on the mid-dorsal cranium similar to that of *Pherohapsis, Mantophryne lateralis, M. louisiadensis* and *Genyophryne*, but narrower. Whether the evolution of the sagittal crest of *Asterophrys* followed a pattern similar to the ontogeny of the crest in *P. doriae*, or occurred by lateral compression of an exostosed plateau is unknown.

Character 28. Fusion and expansion of the vomero-palatine. Though many states occur in the Microhylidae (Parker 1934; Carvalho 1954) (Fig. 19), two appear relevant to this study: (0) vomero-palatine not forming a large plate extending from a median suture to the maxillae (Microhylidae, except Asterophryinae and Genyophryninae); and (1) vomero-palatine a large plate extending from a median suture to the maxillae (Asterophryinae and Genyophryninae) (Figs 14B, D, 15B, D, F, 16B, D, 17B, D, 18B).

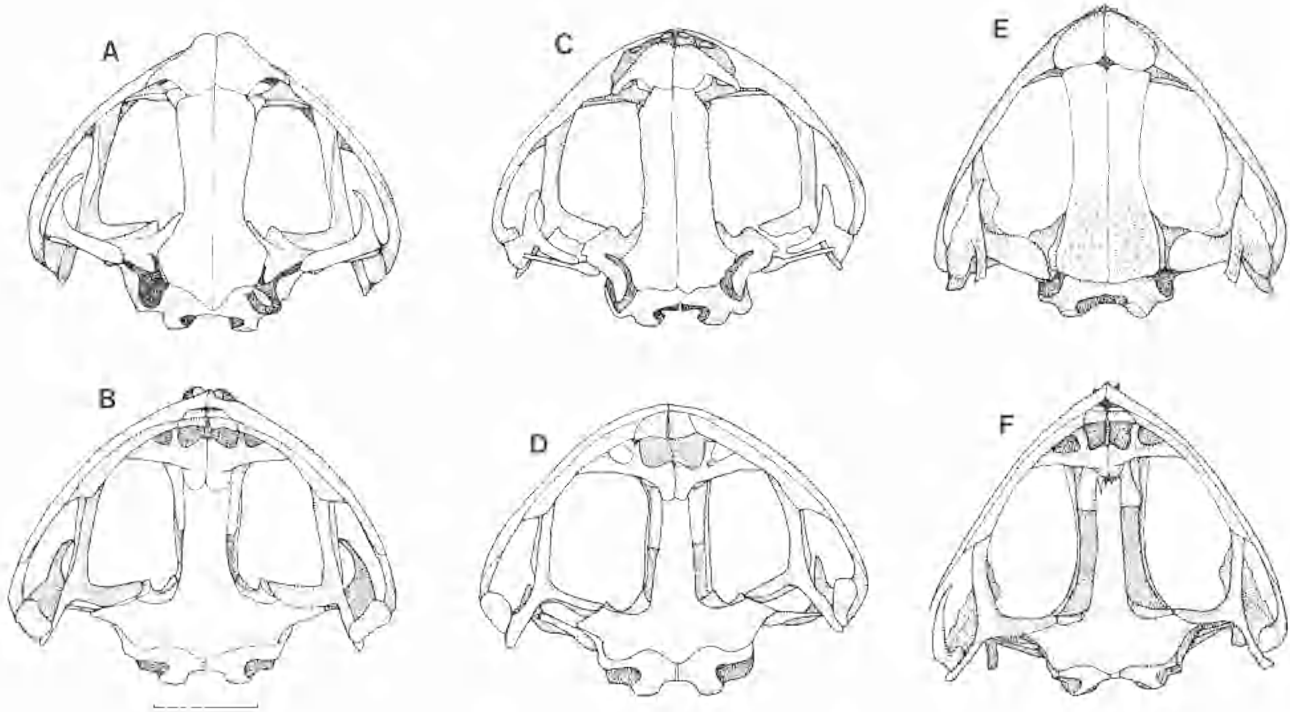Though the primitive state of the microhylids is

FIG. 15. A. Dorsal and B. ventral views of the skull of *Phrynomantis stictogaster* SAMA R 20886; C. Dorsal and D. ventral views of the skull of *Phrynomantis doriae* SAMA R6284; E. Dorsal and F. ventral views of the skull of *Mantophryne lateralis* AUZ D737. Scale bar = 5 mm.

unclear, it is unlikely that it is the unique state exhibited by the New Guinea subfamilies, and State (1) is considered derived.

Character 29. Lateral expansion of the vomero-palatine. Two states occur in the Papuan microhylids: (0) vomero-palatine not expanded close to its lateral articulations (Genyophryninae, except *Cophixalus pansus* and *Genyophryne*) (Fig. 18B); and (1) vomero-palatine expanded laterally (Asterophryinae, *C. pansus* and *Genyophryne*) (Figs 14B, D, 15B, D, F, 16B, D, 17B, D).

As the vomero-palatine of other microhylids are reduced relative to the Papuan microhylids, the unexpanded condition, State (0) is likely to be primitive.

Character 30. Extent of median expansion of the vomero-palatine. Two states occur among the astero-phryines: (0) expansion moderate (*Asterophrys, Hylophorbus, Mantophryne, Pherohapsis* and *Phrynomantis*) (Figs 15B, D, F, 16B, D, 17D); and (1) expansion large (*Barygenys, Xenobatrachus* and *Xenorhina*) (Figs 14B, D).

State (0) is shared by the genyophrynines (Figs 17B, 18B), and is primitive among the asterophryines.

Character 31. Occurrence of spike-like odontoids on the vomero-palatine. Two states occur among the asterophryines: (0) spikes absent (Asterophryinae, except *Xenobatrachus*); and (1) spikes present (*Xenobatrachus*) (Fig. 14D).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 32. Width of the cultriform process of the parasphenoid. Two states occur among the Papuan

microhylids: (A) cultriform process relatively narrow, less than 1/2 of the width of the frontoparietals (Asterophryinae, except *Barygenys, Xenobatrachus* and *Xenorhina*; Genyophryninae, except *Genyophryne*) (Figs 15B, D, F, 16B, D, 17D, 18B); and (B) cultriform process broad, more than 2/3 of the width of the frontoparietals (*Barygenys, Xenobatrachus, Xenorhina* and *Genyophryne*) (Figs 14B, D, 17B).

Both states are shared by the other microhylids examined, and it is not possible to assign polarities to this character.

Character 33. Extent of the articulation of the pterygoid with the prootic. Two states occur in the Papuan microhylids: (0) articulation short (Genyophryninae, except *Genyophryne*) (Fig. 18B); and (1) articulation long (Asterophryinae and *Genyophryne*) (Figs 14B, D, 15B, D, F, 16B, D, 17B, D).

State (0) is shared by the other microhylids examined, and is primitive among the Papuan microhylids.

Character 34. Development of the quadratojugal. Two states occur in the Papuan microhylids: (0) quadratojugal poorly developed, articulation with the maxilla brief or lacking (Genyophryninae, except *Genyophryne*) (Fig. 18B); and (1) quadratojugal well developed, articulation with the maxilla long (Astero-phryinae and *Genyophryne*) (Figs 14B, D, 15B, D, F, 16B, D, 17B, D).

State (0) is shared by the other microhylids examined, and is primitive among the Papuan microhylids.

Character 35. Relationship between the squamosal and the maxilla. Two states occur among the Papuan microhylids: (0) no contact between the zygomatic
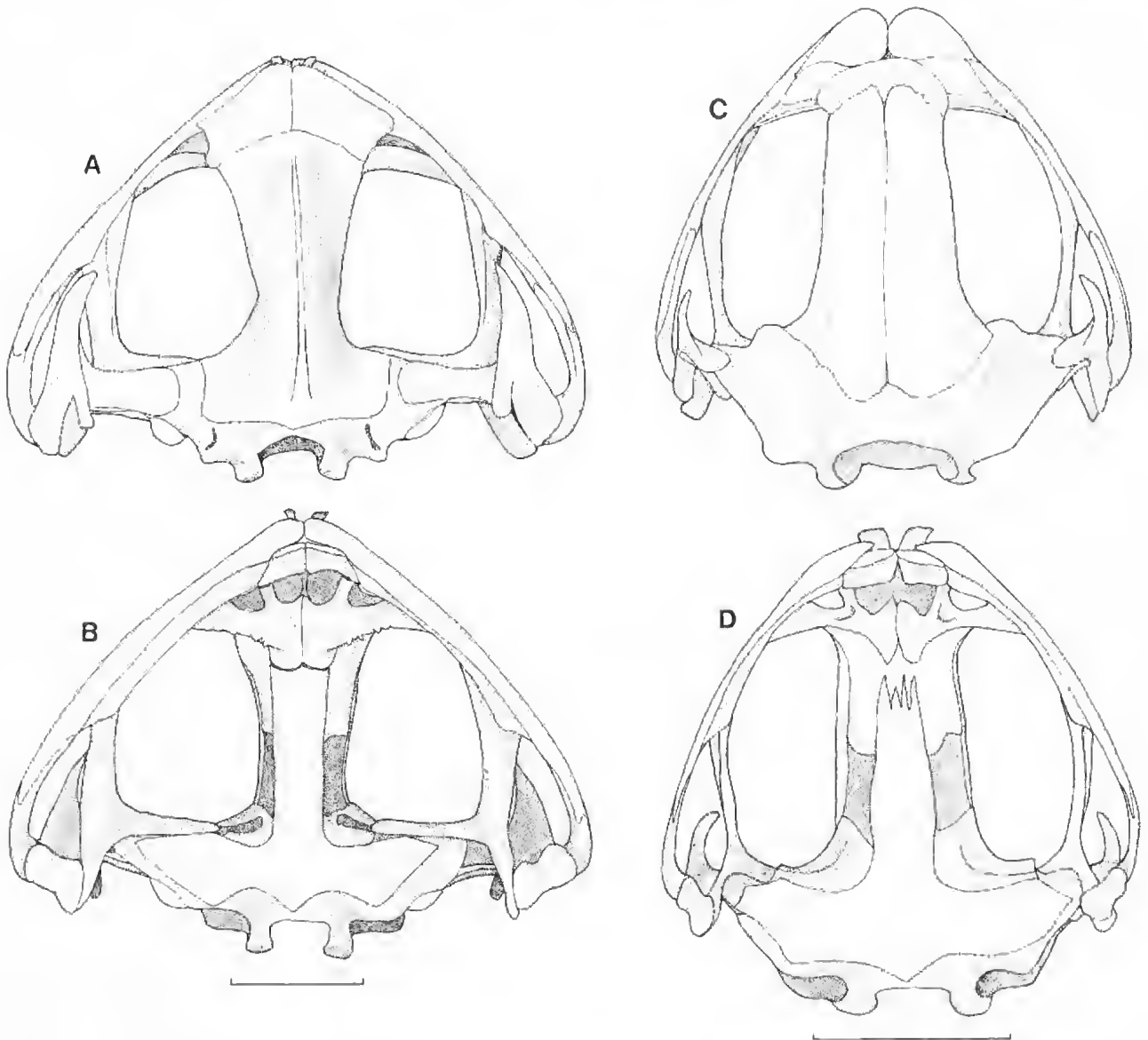
FIG. 16. A. Dorsal and B. ventral views of the skull of *Asterophrys turpicula* RMNH 16655; C. Dorsal and D. ventral views of the skull of *Hylophorbus r. rufescens* AUZ D738. Scale bar = 5 mm.

ramus and the maxilla (Genyophryninae, except *Genyophryne*; Asterophryinae, except *Asterophrys* and *Pherohapsis*); and (1) ventral margins of the zygomatic ramus and the squamosal shaft in contact with the dorsal margins of the quadratojugal and the maxilla, and the lateral surface of the resultant sheet of bone exostosed (*Asterophrys, Pherohapsis* and *Genyophryne*) (Figs 15A, 17A).

State (0) is shared by the other microhylids examined, and is primitive among the Papuan microhylids. The small specimen of *Asterophrys* that I examined lacks this connexion (Figs 16A, B) but Zweifel (1972) reports and figures it in other specimens.

Character 36. Occurrence of a posterad extension of the zygomatic ramus of the squamosal. Two states occur among the asterophryines: (0) no posterad extension, or else a slight flange on the posterior surface of the base of the otic ramus (*Barygenys, Hylophorbus, Phrynomantis, Xenobatrachus, Xenorhina, Mantophryne infulata, M. louisiadensis*);

and (1) posterad expansion of the zygomatic ramus (*Asterophrys, Pherohapsis* and *Mantophryne lateralis*) (Figs 15E, 16A, 17C).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 37. Nature of the otic ramus of the squamosal. Four states occur among the Papuan microhylids: (0) dorsal surface of the otic ramus a flat plate continuous with the anterior surface of the medial flange of the squamosal shaft; ramus short, not extending to articulate with the crista parotica (Genyophryninae, except *Choerophryne*, the *darlingtoni*-group and *Genyophryne*) (Fig. 18A); (1) as in State (0), but ramus longer, overlying the crista parotica (*Asterophrys, Hylophorbus, Mantophryne, Pherohapsis, Xenobatrachus, Xenorhina, Choerophryne*, the *darlingtoni*-group and *Genyophryne*) (Figs 14C, 15E, 16A, C, 17C); (1') dorsal surface of the otic ramus continuous with the lateral shaft; ramus extending medially; medial flange of shaft reduced
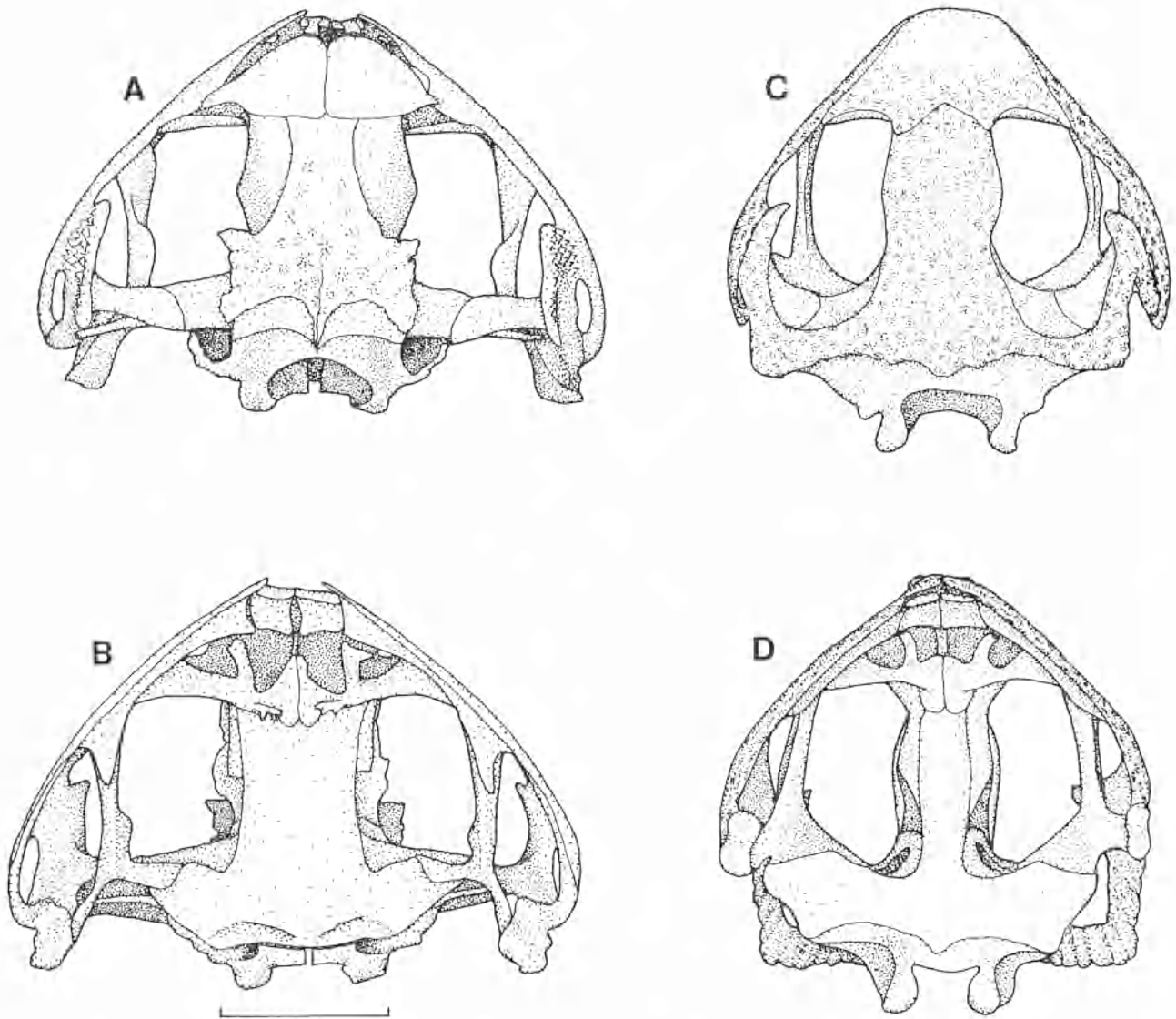
FIG. 17. A. Dorsal and B. ventral views of the skull of *Genyophryne thomsoni* UPNG 5130; C. Dorsal and D. ventral views of the skull of *Pherohapsis menziesi* UPNG 2579. Scale bar — 5 mm.

(*Phrynomantis*) (Figs 15A, C); and (1") dorsal surface of the otic ramus continuous with the anterior surface of the medial flange; ramus not a flat plate, but folded so that it forms a sheet covering the anterior surfaces of the otic capsule; just extending to articulate on the anterodorsal margin of the crista parotica (*Barygenys*) (Fig. 14A).

State (0) occurs in the other microhylids and appears to be primitive among the Papuan microhylids. State (1) is likely to have been derived directly from State (0), but is unlikely to have formed an intermediate stage in the evolution of State (1') as State (1) involves an even greater expansion of the medial flange of the squamosal shaft than does State (0), and State (1') involves a reduction of the medial flange to a ridge on the shaft. In State (1") the medial flange is expanded and this state may have been derived from either State (0) or State (1). The polarity of this character is either 1" — 0¦ or 1' — 0 — 1 — 1".

Character 38. Occurrence of an anterior connexion between the partes faciales of the maxillae. Four states

occur among the Papuan microhylids (Fig. 20): (0) partes faciales produced antero-medially to overlap the premaxillae slightly; direct ligamentous connexion between the tips of the partes faciales lacking (Genyophryninae, except *Genyophryne*); (1) partes faciales produced anteromedially to overlap the premaxillae slightly, but more than in State (0); dense ligamentous connexion between the tips of the partes faciales (*Genyophryne* and *Hylophorbus*; (2) partes faciales broadly overlapping the premaxillae; connexion by dense ligaments or by a median suture (Asterophryinae, except *Barygenys* and *Hylophorbus*; and (1') no anteromediad projection of the partes faciales, no overlap of the premaxillae, no ligamentous connexion (*pace* Zweifel, 1971); premaxillae narrow, compressed between the maxillae (*Barygenys*).

State (0) occurs in other microhylids, and is primitive among the Papuan microhylids. State (1') is more likely to have been derived from State (0) than from State (1) or (2), as State (1'), which is associated with three thickened ridges of skin on the snout corresponding
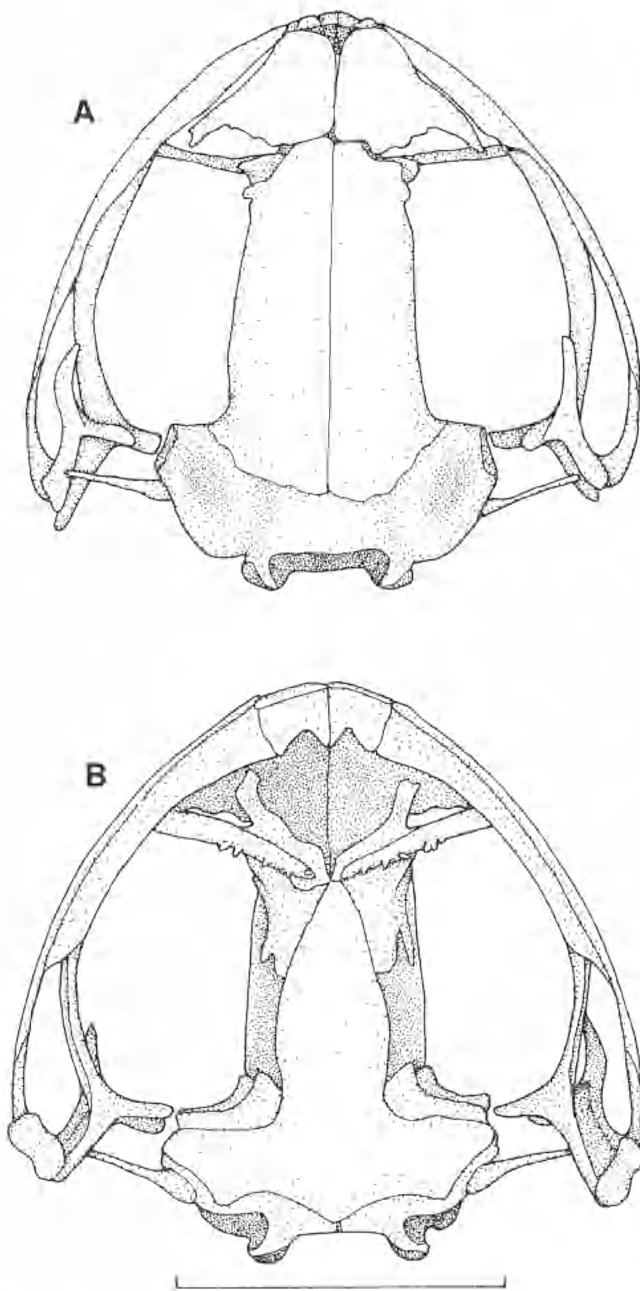
FIG. 18. A. Dorsal and B. ventral views of the skull of *Cophixalus riparius* SAMA R5216a. Scale bar = 5 mm.
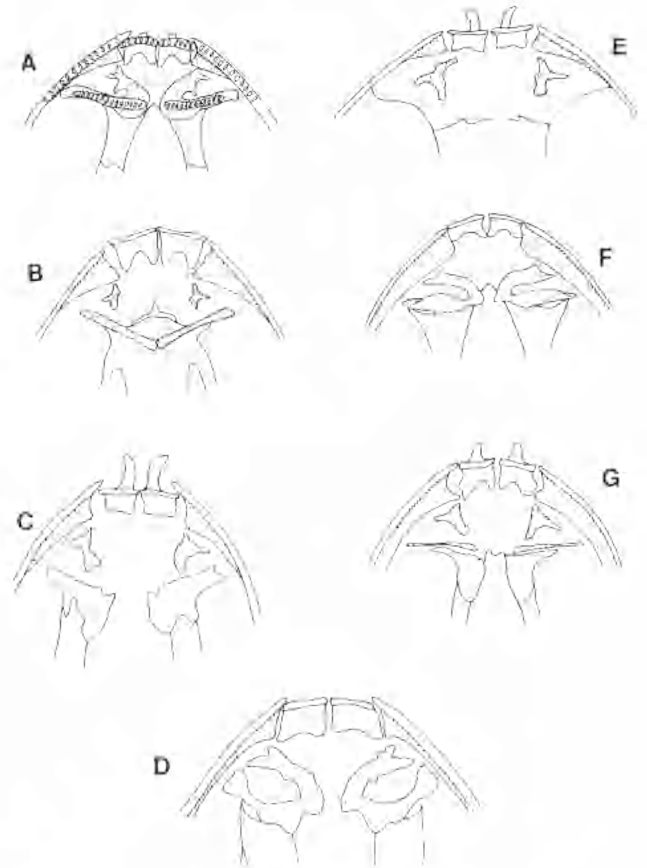

FIG. 19. Ventral views of anterior bones of the skull of various microhylids, with the vomero-palatine and palatine shelf of the maxillary shaded. (A) *Calluella guttalata*; (B) *Chaperina fusca*; (C) *Elachistocleis* sp.; (D) *Glyphoglossus molossus*; (E) *Kalophrynus pleurostigma*; (F) *Kaloula pulchra*; (G) *Microhyla pulchra* (partly after Parker, 1934).

with sites of articulation of the maxillae and premaxillae, represents a radically different mode of snout reinforcement from that represented by States (1) and (2). State (1) is likely to have been derived from State (0) by extension of the anteromediad processes of the partes faciales and the establishment of a ligamentous connexion between them. The polarity of this character is thus 1' ← 0 → 1 → 2.

I regard States (1) (possessed by *Genyophryne* and *Hylophorbus*) and (2) (*symphygnathy*) as differing only in degree, and consider the distinction between them somewhat arbitrary. Mehely (1901), Parker (1934) and Zweifel (1971, 1972), on the other hand, regarded the distinction as, to varying degrees, crucial. The difference between my appraisal and that of Mehely

and Parker may arise in part from my having access to a large number of cleared and double-stained specimens, in which the presence or absence of ligamentous connexions is more obvious than in dried skeletons. Zweifel (1971) noted ligamentous connexions in *Genyophryne* (and implied their presence in *Barygenys* and *Hylophorbus*), but decided that the degree of closeness of contact of the maxillae is a more important indicator of relationships. I contend that closeness of contact has been overemphasised, as in some "symphygnathine" species, e.g., *Mantophryne infulata*, the distance between the partes faciales (up to 0.3 mm) approaches that of *Genyophryne* and *Hylophorbus*, and in *Genyophryne* and *Hylophorbus* the partes faciales are closer than in those genyophrynines exhibiting the State (0) condition. Whether or not my contention that the condition of *Genyophryne* and *Hylophorbus* is close to that exhibited by those asterophryines of State (2) condition is accepted, the possession by *Genyophryne* and *Hylophorbus* of a state different from State (0) and intermediate between States (0) and (2) is indisputable.

Character 39. Occurrence of a posteromediad process of the anterior margin of the palatal shelf of the maxilla. Two states occur among the astero-phryines: (0) process lacking (*Asterophrys, Barygenys,*

FIG. 21. Anterior views of the mandibles of (A) *Rana grisea* AUZ; (B) *Genyophryne thomsoni* UPNG 5130; (C) *Sphenophryne schlaginhaufeni* AUZ B733; (D) *Kaloula pulchra* FMNH 175952; (E) *Barygenys* sp. nov. AA 11171. Scale bar = 5 mm.
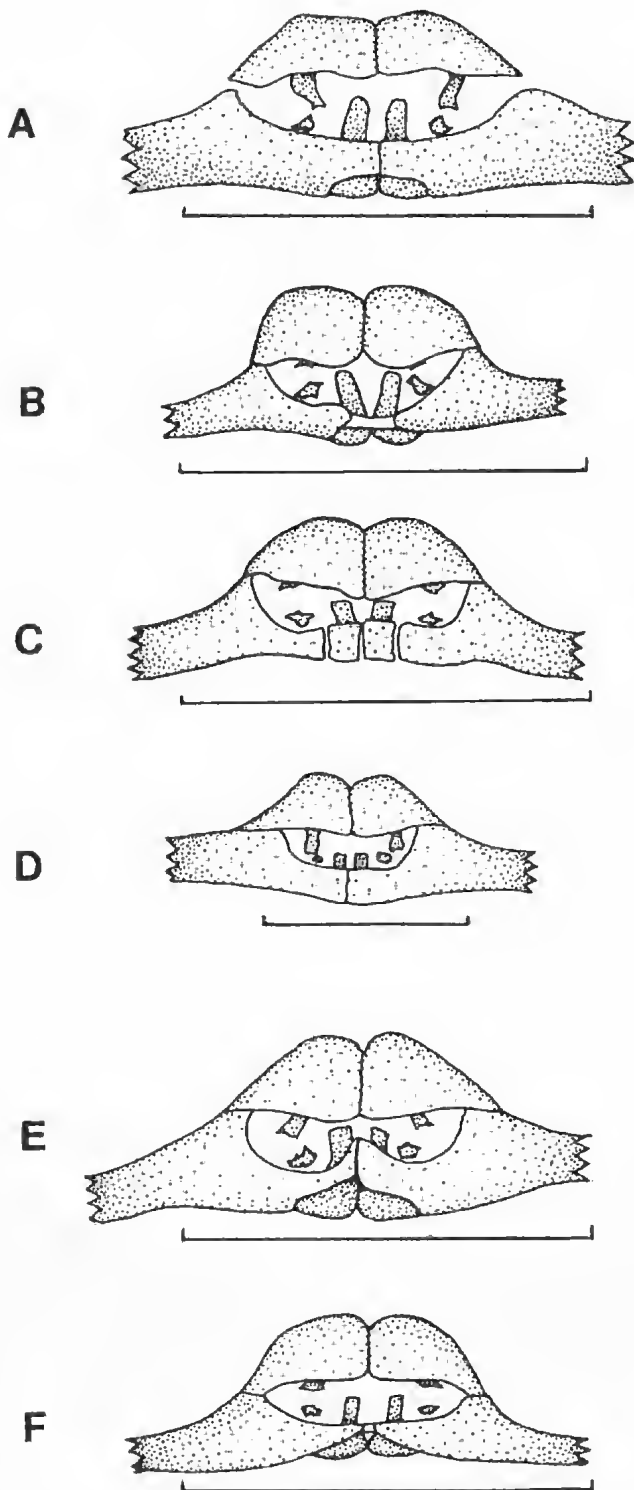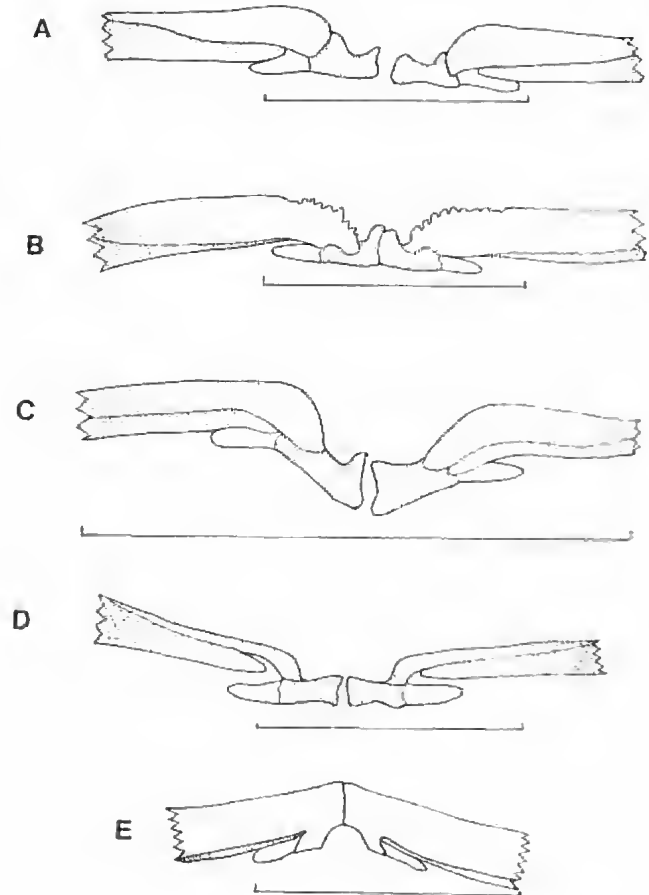
FIG. 20. Anterior view of the bones of the snouts of (A) *Phrynomantis humicola compta* SAMA R9387a; (B) *Hylophorbus r. rufescens* AUZ D738; (C) *Barygenys atra* UPNG 3836; (D) *Xenobatrachus giganteus* UPNG 5680; (E) *Mantophryne lateralis* AUZ D737; (F) *P. infulata* AMNH 66685. Scale bar = 5 mm.

Hylophorbus, Pherohapsis, Mantophryne and *Phrynomantis*); and (1) process present (*Xenobatrachus* and *Xenorhina*) (Fig. 14D).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 40. Calcification of the nasal capsule. Two states which occur among the asterophryines are considered: (0) anterior portion of the nasal capsule cartilaginous (*Asterophryinae*, except *Barygenys*); and (1) anterior portion of the nasal capsule calcified to form a calcified arc between the septomaxillaries (*Barygenys*) (Fig. 20C). State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 41. Relations of the dentaries and mentomeckelians. Two states occur in the Papuan microhylids: (0) dentary and mentomeckelian not fused; mentomeckelians lying on the rim of the mandible between the dentaries; angle between the long axes of the mentomeckelians obtuse (Genyophryninae) (Fig. 21B, C); and (1) dentary and mentomeckelian fused; mentomeckelians largely or entirely excluded from the rim of the mandible by the dentaries; angles between the long axes of the mentomeckelians acute (Asterophryinae) (Fig. 21E).

State (0) is shared by ranoids and other microhylids (Figs 21A, D), and is primitive among the Papuan microhylids. State (1) embraces the condition in *Hylophorbus* and *Mantophryne infulata*, in which the dentaries do not meet, and that of other asterophryines in which they do (the symphygnathine condition), as I consider this difference a matter of degree only, and not as indicative of relationships as the similarities of
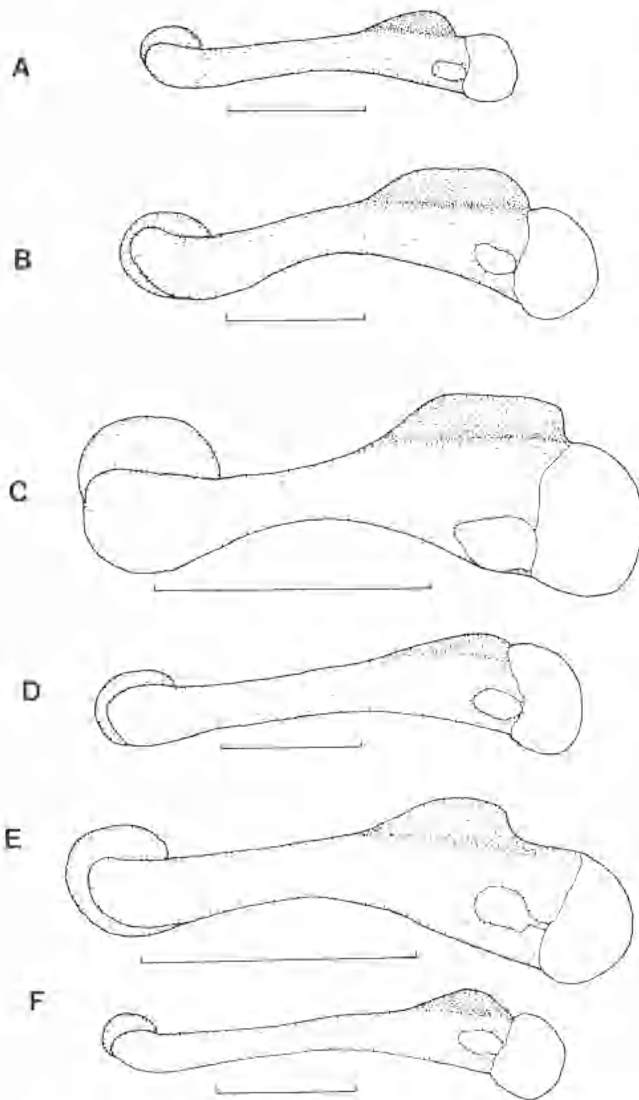
FIG. 22. Right humerus of (A) *Phrynomantis humicola compta* SAMA R9387a; (B) *Xenobatrachus giganteus* UPNG 5680; (C) *Barygenys atra* UPNG 3836; (D) *Asterophrys turpicula* RMNH 16655; (E) *Genyophryne thomsoni* UPNG 5130; (F) *Cophixalus riparius* SAMA R5216a. Scale bar = 5 mm.

the conformation of the mentomeckelians and the relationship between the dentary and the mentomeckelian, which are unique to the Asterophryinae.

Character 42. Degree of development of the humerus. Two states occur among the Papuan microhylids: (A) humerus relatively straight; crista ventralis moderately developed (Asterophryinae, except *Barygenys, Xenobatrachus* and *Xenorhina*; Genyophryninae, except *Genyophryne*) (Figs 22A, D, F) (B) humerus curved; crista ventralis well developed (*Barygenys, Xenobatrachus, Xenorhina* and *Genyophryne*) (Figs 22B, C, E).

Both states occur among the other microhylids, and so polarities cannot be assigned. No noticeable sexual difference occurs in this character.

Character 43. Reduction of the pectoral girdle. Four states occur among the Papuan microhylids (Fig. 23): (0) procoracoids present; clavicle extending laterally to articulate with scapula (*Sphenophryne*); (1) procoracoids present; clavicles not extending as far

laterally as the scapula (*Oreophryne*); (2) procoracoids present; clavicles absent (*Genyophryne*); and (3) procoracoids absent; clavicles absent (Asterophryinae, *Choerophryne, Cophixalus, Copiula* and the *darlingtoni*-group).

Reduction of the pectoral girdle occurs in other microhylid subfamilies (Fig. 23) and in the Ranidae, and is believed to have occurred independently several times. A complete pectoral girdle is generally regarded as primitive, e.g., Trueb (1973), Laurent (1979). Certainly the reacquisition of elements of the pectoral girdle lost in the evolutionary history of the genyophrynines is less likely than the alternative, a progressive loss of elements of the pectoral girdle.

Character 44. Nature of the vertebral column. Two states occur among the Papuan microhylids: (A) all presacral vertebrae procoelous (vertebral column procoelous) (Genyophryninae); and (B) all presacral vertebrae procoelous except the eighth, which is opisthocoelous (vertebral column diplasiocoelous) (Asterophryinae). Both states occur in ranoids (Duellman 1975) and other microhylids, and although State (B) is the more common (Parker 1934) it is not possible to ascribe polarities to this character on the basis of outgroup analysis. Parker (1934) and Carvalho (1954) demonstrated variation in this character within the Microhylinae. Whether this indicates that this character is of little significance in the Microhylidae as a whole (Savage 1973) is unclear.

Character 45. Occurrence of a dorsal crest on the ilium. Two states occur among the asterophryines (Fig. 24): (0) ilial shaft lacking a dorsal crest (*Barygenys* and *Phrynomantis*); and (1) ilial shaft bearing a dorsal crest (*Asterophrys, Hylophorbus, Mantophryne, Pherohapsis, Xenobatrachus* and *Xenorhina*).

State (0) is shared by the genyophrynines, and is primitive among the asterophryinae.

Character 46. Nature of the ilio-sacral articulation. Two states occur in Papuan microhylids: (A) articulation indirect, a dorsal ligament connecting the ilial shafts; this is the type I articulation of Emerson (1979) (*Hylophorbus, Pherohapsis, Mantophryne infulata, M. lateralis, Choerophryne, Cophixalus, Copiula, Oreophryne* and the *darlingtoni*-group); and (B) articulation by a ligament attaching to the dorsal surface of the sacral diapophysis close to its base; this is the type IIA articulation of Emerson (1979) (*Asterophrys, Barygenys, Phrynomantis, Mantophryne louisiadensis, Xenobatrachus, Xenorhina, Genyophryne* and *Sphenophryne*).

Both states occur among the other microhylids, and it is not possible to ascribe polarities to this character.

Character 47. Eye-size. Two states occur among the Papuan microhylids: (0) eye relatively large; E : S-V > 0.090 (Asterophryinae, except *Barygenys, Xenobatrachus, Xenorhina* and *Phrynomantis doriae* — see below; Genyophryninae, except *Copiula* and *Genyophryne*); and (1) eye relatively small; E: S-V <
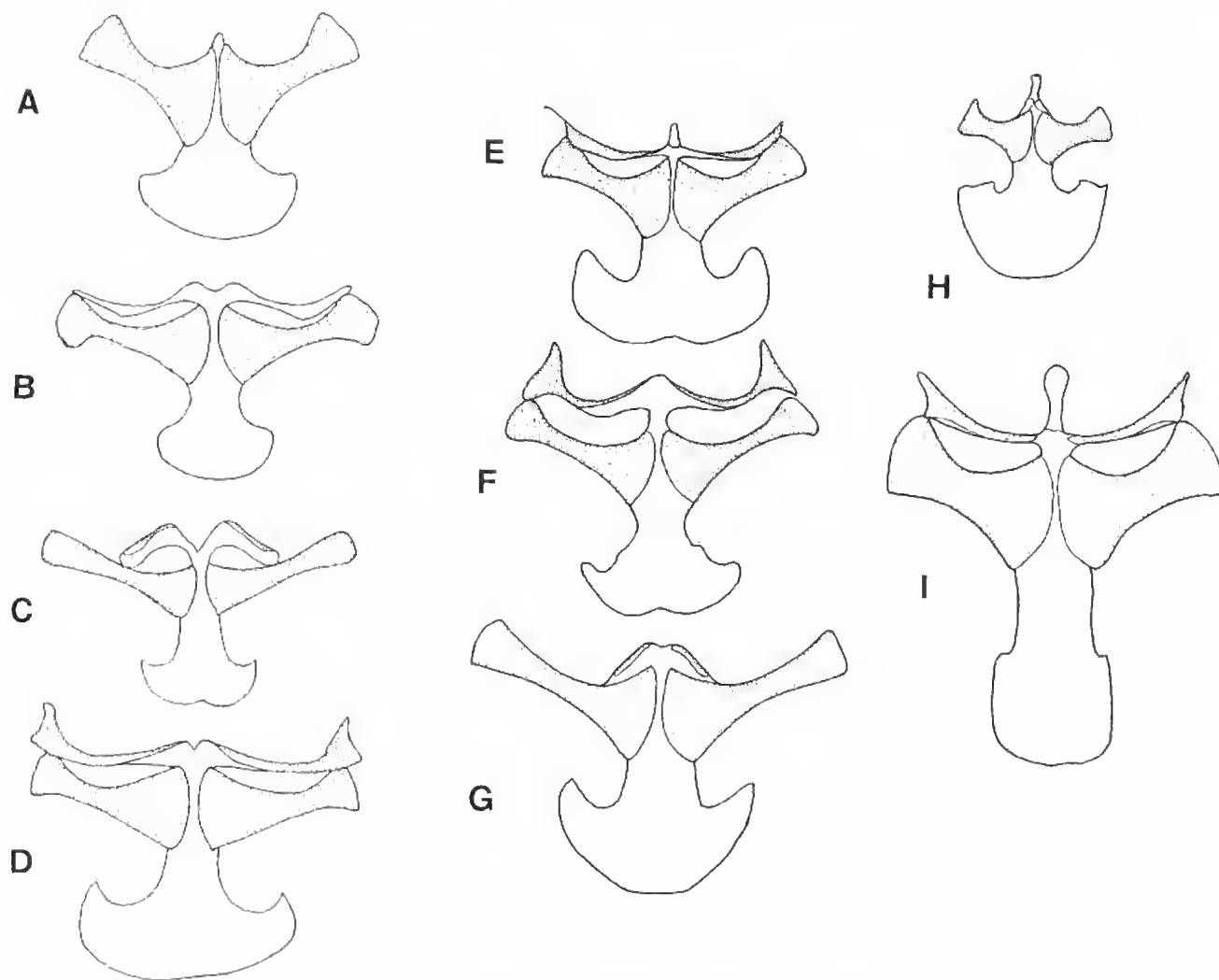
FIG. 23. Ventral views of the pectoral girdles of (A) *Cophixalus ornatus* AUZ D740; (B) *Genyophryne thomsoni* UPNG 5130; (C) *Oreophryne biroi* SAMA R10899; (D) *Sphenophryne cornuta*; (E) *Calluella guttulata*; (F) *Chaperina fusca*; (G) *Elachistocleis* sp.; (H) *Kaloula pulchra*; (I) *Kalophrynus pleurostigma* (D-I modified after Parker, 1934).

0.090 (*Barygenys, Xenobatrachus* except *X. ocellatus, Xenorhina, Copiula* and *Genyophryne*).

The eyes of the genera exhibiting State (1) are generally smaller than those of the other microhylids examined and State (0) is regarded as primitive among the Papuan microhylids.

Zweifel (1972) characterizes *Phrynomantis doriae* as a small-eyed frog, with a relative eye size conforming to the ratios seen in *Xenorhina*. The sample sizes for populations I examined are too small to document conclusively an ontogenetic trend to smaller relative eye sizes within asterophryine species, but a trend to smaller relative eye size in larger species within genera is apparent. Figures 25 and 26 show the logs of eye diameter to snout-vent length plotted against snout-vent length in *Phrynomantis* and *Xenorhina* and *Xenobatrachus* combined, with the ratios of specimens of *P. doriae* plotted on both graphs. Clearly, although the eye of *P. doriae* is smaller that that of other *Phrynomantis*, it conforms better to the trend to smaller relative eye size in larger *Phrynomantis* better

than to the similar trend in *Xenorhina* and *Xenobatrachus*.

Character 48. Development of subarticular tubercles. Two states occur among the asterophyrines: (0) subarticular tubercles poorly developed or absent (*Barygenys, Phrynomantis, Xenobatrachus* and *Xenorhina*); and (1) subarticular tubercles well developed (*Asterophrys, Hylophorbus, Mantophryne* and *Pherohapsis*).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 49. Adherence of the tongue. Two states occur among the Papuan microhylids: (0) tongue free posteriorly, for at least 1/4 of its length (Genyophryninae); and (1) tongue adherent posteriorly (Asterophryinae).

Although both states occur among the other microhylids, only State (0) appears to be found among the ranoids. For this reason I regard State (0) as primitive among the Papuan microhylids.

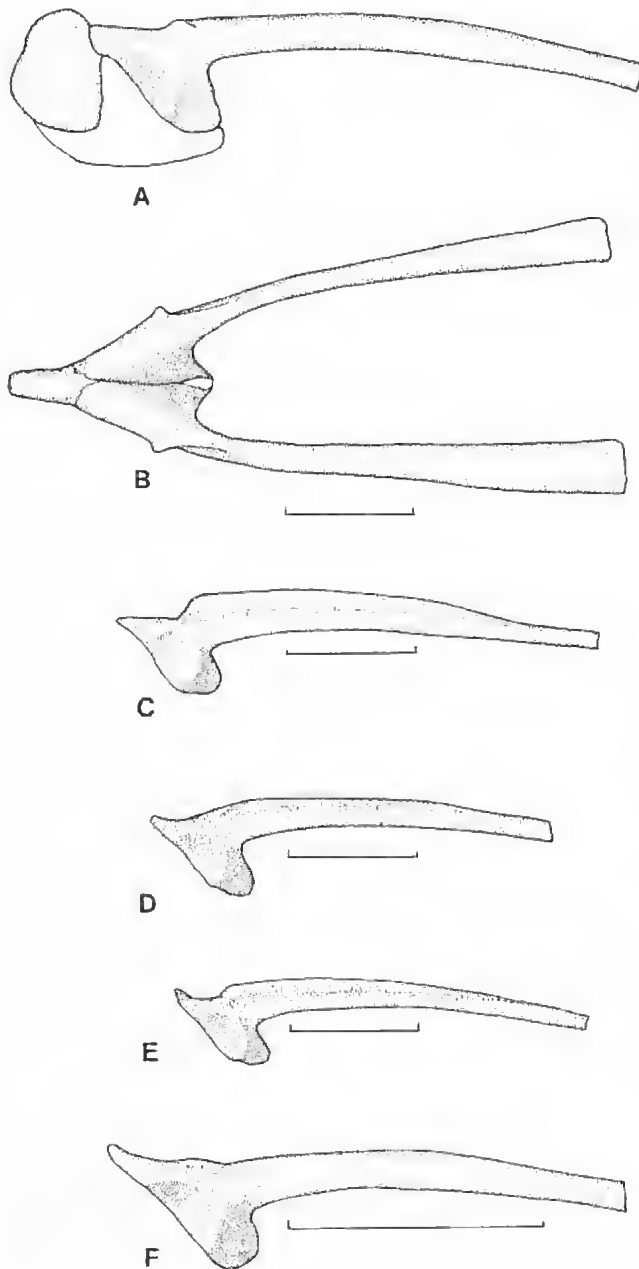*Character 50.* Uniformity of the tongue surface. Two

FIG. 24. A. Right lateral and B. dorsal views of the pelvic girdle of *Phrynomantis stictogaster* SAMA R20886; lateral view of right ilium of (C) *Mantophryne lateralis* AUZ D737; (D) *Xenobatrachus giganteus* UPNG 5680; (E) *Hylophorbus r. rufescens* AUZ D738; (F) *Barygenys atra* UPNG 3836. Scale bar = 5 mm.
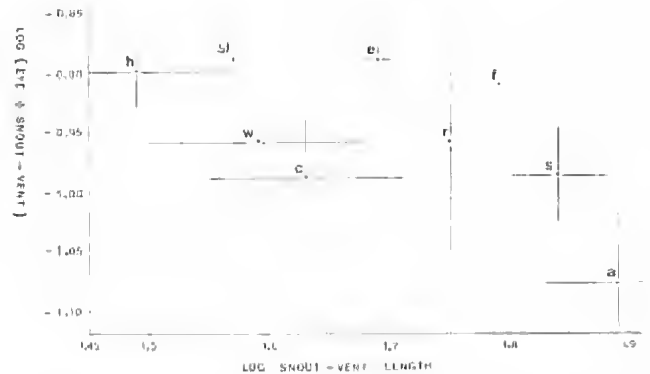

FIG. 25. Graph of log of eye to snout-vent length ratio against log of snout-vent length of *Phrynomantis* species. Means and standard deviations are shown for each species. Legend: a, *Phrynomantis doriae*; c, *P. humicola compta*; e, *P. eurydactyla*; f, *P. fusca*; h, *P.h. humicola*; r, *P. robusta*; s, *P. stictogaster* sl, *P. slateri*; w, *P. wilhelmana*.
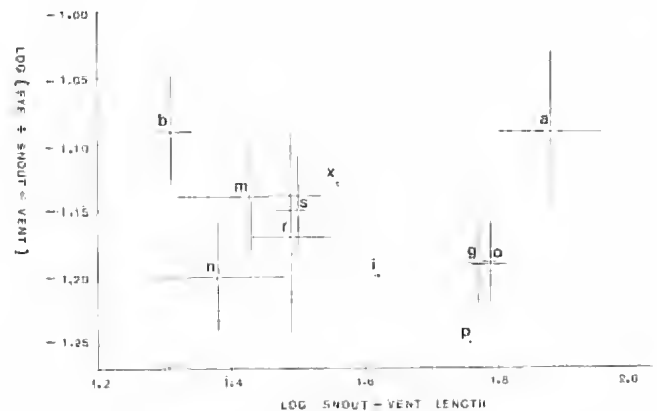

FIG. 26. Graph of the log of eye to snout-vent ratio against the log of snout-vent length in species of *Xenobatrachus* and *Xenorhina*, including *Phrynomantis doriae* for comparison. Means and standard deviations are shown for each species. Legend: g, *Xenobatrachus giganteus*; m, *X. mehelyi*; o, *X. obesus*; r, *X. rostratus*; s, *X. subcroceus*; b, *X. bouwensi*; i, *X. similis*; n, *X. mininna*; p, *X. parkerorum*; x, *X. oxycephala*; a, *Phrynomantis doriae*.

states occur among the Papuan microhylids (Fig. 27): (0) tongue uniformly pitted and glandular (Genyophryninae, except *Cophixalus riparius*); and (1) tongue divided into an anterior smooth, non glandular section and a posterior glandular section (Asterophryinae and *Cophixalus riparius*).

State (0) occurs in other microhylids, and is primitive among the Papuan microhylids. *C. riparius* is the largest of the genyophrynines examined, and the occurrence of this character may be related to ontogeny, as it is lacking in juvenile specimens of *Phrynomantis h. humicola*.

Character 51. Nature of the glandular surface of the tongue. Two states occur among the asterophryines: (0)

glandular surface more or less uniformly pitted (*Asterophrys, Barygenys, Hylophorbus, Mantophryne, Pherohapsis* and *Phrynomantis*) and (1) glandular surface bearing deep longitudinal striae (*Xenobatrachus* and *Xenorhina*) (Fig. 27).

State (0) is shared by the genyophrynines, and is primitive.

Character 52. Possession of a pair of warts on the chin. Two states occur among the asterophryines: (0) warts absent (*Barygenys, Hylophorbus, Phrynomantis, Xenobatrachus* and *Mantophryne infulata*); and (1) two warts or wart-like protrusions on the chin (*Asterophrys, Pherohapsis, Mantophryne lateralis, M. louisiadensis*).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 53. Number of denticles on the posterior prepharyngeal fold. Two states occur among the asterophryines: (0) large number of denticles, usually far more than 10 except in a few specimens (*Asterophrys, Hylophorbus, Mantophryne,*
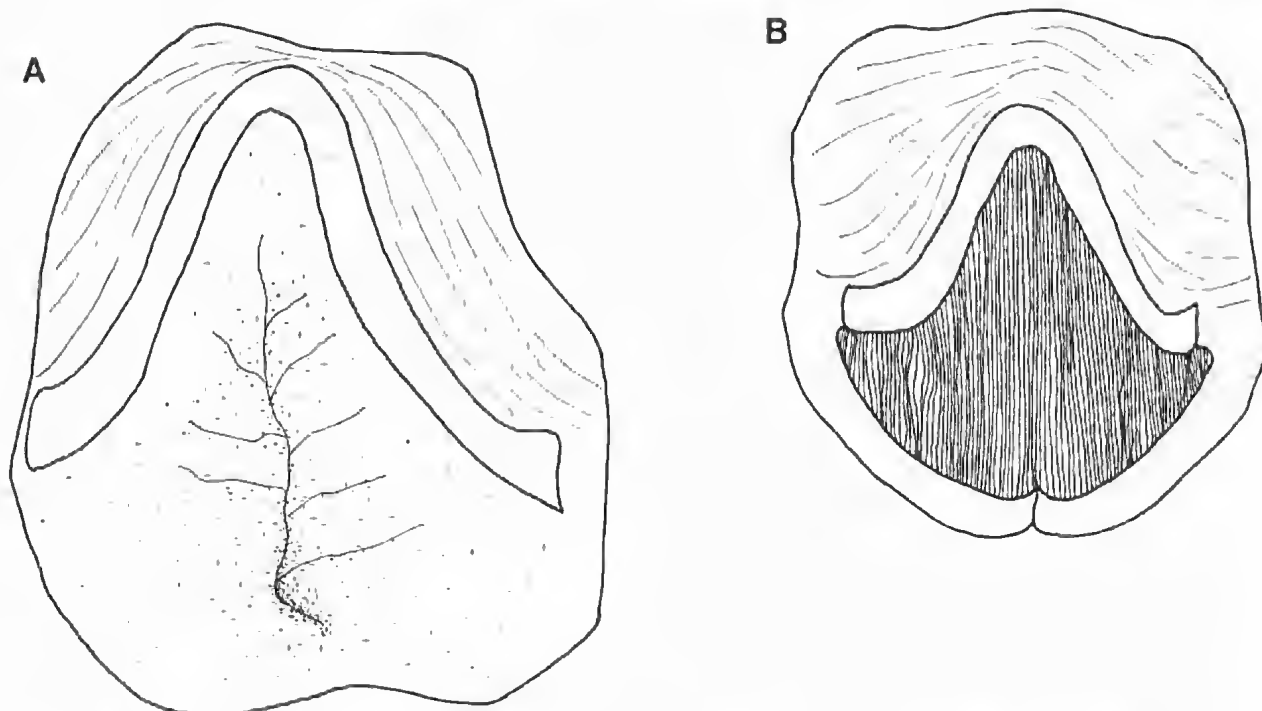
FIG. 27. Dorsal surfaces of the tongues of (A) *Barygenys atra* UPNG 3836; (B) *Xenobatrachus giganteus* UPNG 5680.

Pherohapsis and *Phrynomantis*); and (1) small number of denticles, less than 10 (*Barygenys, Xenobatrachus* and *Xenorhina*).

State (0) is shared by the genyophrynines, and is primitive among the asterophryines.

Character 54. Life history. There are many states of life history among the Microhylidae (Parker 1934), but two are considered here: (0) larva possessing an operculum; metamorphosis usually completed outside the egg capsule (Microhylidae, except Asterophryinae and Genyophryninae); and (1) larva lacking an operculum; metamorphosis completed within the egg capsule (Asterophryinae and Genyophryninae).

State (0) is the usual condition of frogs, and is primitive.

Occurrence of digital grooves and discs: Zweifel (1972) noted that the occurrence of grooves and discs varies within genera, particularly *Phrynomantis, Xenobatrachus* and *Xenorhina*. The changes I propose in the composition of the genera do not affect this variability. Zweifel (P. 429) chose to use the development of discs as a phylogenetic character despite identifying "separate parallel trends towards reduction of digital discs" within these genera. He coded *Phrynomantis* and *Xenobatrachus* and *Xenorhina* differently on the grounds that some *Phrynomantis* species which possess discs possess broader discs than *Xenobatrachus* and *Xenorhina* species. I regard this character as too variable for use in a phylogenetic analysis and will not consider it further.

Cladistic Analysis

Here hypotheses are presented relating to the monophyly of groups of microhylids, and the evidence

for and against these hypotheses, leading to the establishment of a cladogram. Throughout this section reference is made to the polarities of characters discussed in the previous section summarised in Table 4, and numbers in parentheses are references to the number ascribed to a particular character in the previous section.

Hypothesis 1. Monophyly of the Papuan microhylids

The monophyly of the Papuan microhylids has not been questioned since Parker's (1934) synthesis. Though I attempted to identify autapomorphies of the Papuan microhylids, I was able to add only one character of dubious polarity (15, number of tendinous inscriptions of the *M. rectus abdominis*) to the two characters (28, development of the vomero-palatine; and 54, life history and larval form) presented by Parker (1934).

On the other hand there is no evidence of conflicting synapomorphies suggesting that either Papuan subfamily forms a natural group with any other subfamily examined.

Hypothesis 2(a). Monophyly of the Asterophryinae and of the Genyophryninae

Zweifel (1972) and Tyler (1979) present the opinion that the Asterophryinae descended from a genyophrynine ancestor. Implicit in this belief is the conclusion that the Genyophryninae form a paraphyletic group, and that the Asterophryinae are monophyletic.

This study yielded no unequivocal evidence of the monophyly of the Genyophryninae. Of the four characters in which the two subfamilies differ consistently, three present evidence for the monophyly of the Asterophryinae, and one is of doubtful polarity.

The hypothesis of asterophryine monophyly is supported by: (a) lack of a set of posteromedially

TABLE 4. SUMMARY OF CHARACTER STATES

Character number	Asterophrys	Barygenys	Hylophorbus	Pherohapsis	Phrynomantis	Xenobatrachus	Xenorhina	Mantophryne	Choerophryne	darlingtoni-group	Cophixalus	Copiula	Genyophryne	Oreophryne	Sphenophryne	Other Microhylidae
1	1'	2'	0	0	1	1'	1'	0	0	0	0	0	+	0	+	0
2	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
3	1	1	1	1	1	1	0/1	1	0	0	0/1	0	0	0	0	0, +
4	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
5	C	B	C	C	A	B	B	C	C	C	A	B	B	A	B	A,B
6	0	1'	0	0	0	1	1	0	—	0	0	0	0	0	0	0
7	1	1	1	1	1	1	1	1	—	0	0	0	1	0	0	0,1
8	1'	1	1'	1'	1'	1'	1	1'	—	0	0	0	1'	0	0	0,1
9	1	0	1	1	1	0	0	1	—	0	0	0	0	0	0	0,1
10	1	1	1	1	0/1	1	1	1	0	0	0	0	0	0	0	0
11	0	0	0	0	0	1	1	0	+	+	0	0	0	0	0	0
12	1	2	0	0	0	2	2	0	0	0	0	0	0	0	0	0
13	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0
14	0	1	0	0	0	0	0	0	—	0	0	0	0	0	0	0
15	A	A	A	A	A	A	A	A	—	A	A	A	A	A	A	A,B
16	0	1	0	0	0	0	0	0	—	0	0	0	0	0	0	0
17	0	1	0	0	0	0	0	0	—	0	0	0	0	0	0	0
18	0	1	0	0	0	1	1	0	—	0	0	0	0	0	0	0,1, +
19	0	1	0	0	0	1	1	0	—	0	0	0	0	0	0	0
20	1	0	1	1	1	1	1	1	—	0	0	0	0	0	0	0
21	B	A	B	A	A	A	A	B	—	A	A	B	A	A	B	A,B
22	1	0	1	1	0	0	0	1	—	0	0	0	0	0	0	0
23	0	1	0	0	0	0	0	0	—	0	0	0	0	0	0	0
24	1	0	1	1	1	1	1	1	—	0	0	0	0	0	0	0
25	1	0	1	1	1	1	1	1	—	0	0	0	0	0	0	0
26	0	0	1	1	0	0	0	1	—	0	0	0	1	0	0	0
27	1	0	0	0	0/1	0/1	0	0	—	0	0	0	0	0	0	0
28	1	1	1	1	1	1	1	1	—	1	1	1	1	1	1	0
29	1	1	1	1	1	1	1	1	—	0	0/1	0	1	0	0	0
30	0	1	0	0	0	1	1	0	+	+	0	0	0	0	0	0
31	0	0	0	0	0	1	0	0	—	0	0	0	0	0	0	0
32	A	B	A	A	A	B	B	A	—	A	A	A	B	A	A	A,B
33	1	1	1	1	1	1	1	1	—	0	0	0	1	0	0	0
34	1	1	1	1	1	1	1	1	—	0	0	0	1	0	0	0
35	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
36	1	0	0	1	0	0	0	0/1	—	0	0	0	0	0	0	0
37	1	1"	1	1	1'	1	1	1	1	1	0	0	1	0	0	0
38	2	1'	1	2	2	2	2	2	—	0	0	0	1	0	0	0
39	0	0	0	0	0	1	1	0	—	0	0	0	0	0	0	0
40	0	1	0	0	0	0	0	0	—	0	0	0	0	0	0	0
41	1	1	1	1	1	1	1	1	—	0	0	0	0	0	0	0
42	A	B	A	A	A	B	B	A	—	A	A	A	B	A	A	A,B
43	3	3	3	3	3	3	3	3	3	3	3	3	2	1	0	0-3
44	B	B	B	B	B	B	B	B	A	A	A	A	A	A	A	A,B
45	1	0	1	1	0	1	1	1	—	0	0	0	0	0	0	0
46	B	B	A	A	B	B	B	A/B	—	A	A	A	B	A	B	A,B
47	0	1	0	0	0	1	1	0	0	0	0	1	1	0	0	0
48	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
49	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0,1
50	1	1	1	1	1	1	1	1	0	0	0/1	0	0	0	0	0
51	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
52	1	0	0	1	0	0	0	0/1	0	0	0	0	0	0	0	0
53	0	1	0	0	0	1	1	0	—	0	0	0	0	0	0	0
54	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0

See text for discussion of State numbers. (—) indicates information is not available; (+) indicates a derived state not discussed in the foregoing character analysis; only states shared with the Asterophryinae and the Sphenophryninae recorded in the "Other Microhylidae" column.

oriented fibres on the dorsal surface of the *M. intermandibularis* (2); (b) a unique structure of the mandible (41); and (c) a tongue that is adherent and superficially complex (49 and 50).

The procoelous vertebral column (44) of genyophrynines may or may not represent an autapomorphy. However, while the hypothesis of paraphyly of a group may be rejected on the evidence of a single autapomorphy, the absence of an autapomorphy does not disprove monophyly: it may reflected the inability of the worker or of the techniques employed to detect autapomorphy. The monophyly of the Genyophryninae can only be disproven by autapomorphies which conflict with the hypothesis of monophyly. Such would be an autapomorphy supporting the monophyly of one or more of the genyophrynine genera with the Asterophryinae.

If, in Figure 28, a genyophrynine genus (G) and the Asterophryinae form a monophyletic group, then the Genyophryninae (S + G) would consist of descendants of a common ancestor (C), but excluding one descendant of (C), the Asterophryinae. That is, the

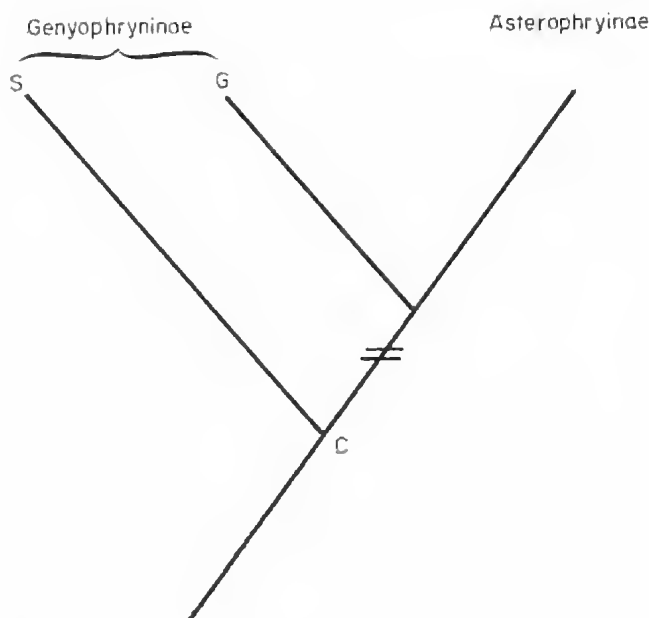Genyophryninae   Asterophryinae

A.

B.

FIG. 28. Phylogeny of the New Guinea microhylids postulated in hypothesis of monophyly 2(b). Abbreviations: C, common ancestor of the Asterophryinae and Genyophryninae; G, Genyophrynine genus sharing synapomorphies with the Asterophryinae; S, other genyophrynine genera. Horizontal strokes through lines indicate acquisition of derived character states.

Genyophryninae would be united only by plesio-morphies and be, by Hennig's (1966) definition, paraphyletic.

Hypothesis 2(b). Monophyly of the group formed by *Genyophryne* and the Asterophryinae

The monotypic genus *Genyophryne* has had a complex history (Introduction), as *Genyophryne thomsoni* possesses a mixture of genyophrynine and asterophryine character states, plus a number of states which do not occur elsewhere in the Microhylidae (e.g. odontoids on the dentary). Consequently, since Parker's (1934) monograph it has been allied with the astero-phryines (Parker 1934), the genyophrynines (Zweifel 1971), and has been the cause of amalgamation of the subfamilies (Savage 1973).

There are three characters of which *Genyophryne* shares with the whole of the Asterophryinae the derived state: lack of a deep slip to the *M. hyoglossus* (7); an extensive articulation of the pterygoid with the prootic (33); and a well developed quadratojugal with a long articulation with the maxilla (34).

Though these characters appear to provide strong evidence of the monophyly of *Genyophryne* plus the Asterophryinae, there are three lines of argument that may be marshalled against this hypothesis.

    (i) Conflict with relationships within the Asterophryinae.

There are two characters of which *Genyophryne* shares the derived condition with all of the asterophryines except *Barygenys*: possession of three *Mm. petrohyoidei posteriores* (8); and extension and
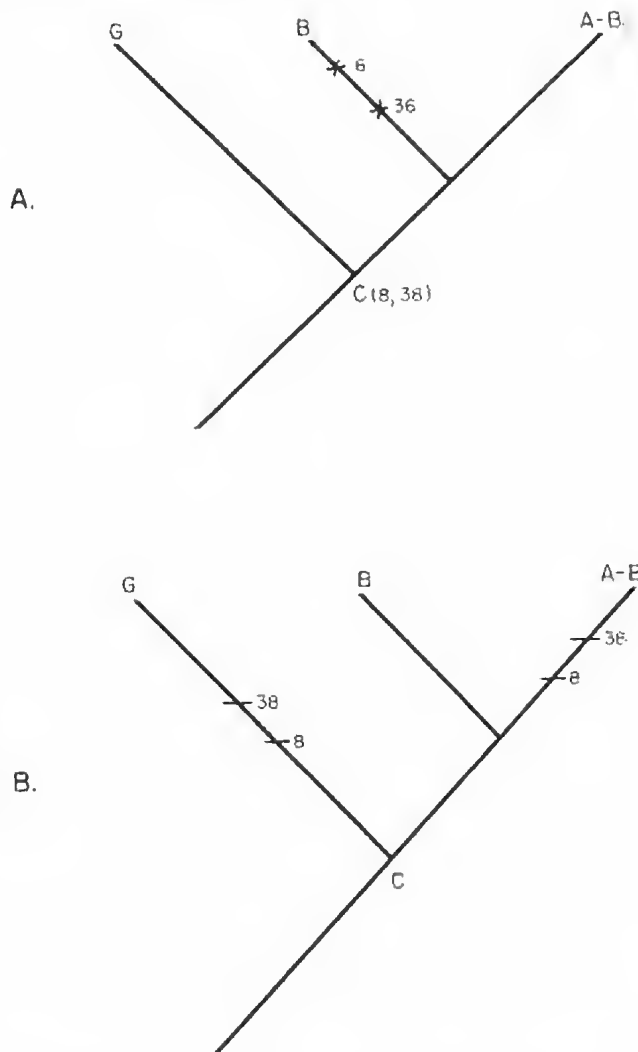
FIG. 29. Postulated relationships of *Genyophryne, Barygenys* and the other Asterophryinae. A. Common ancestor (C) of *Genyophryne* (G), *Barygenys* (B) and the other Asterophryinae (A-B) possesses the derived states of characters 8 and 38, and *Barygenys* undergoes reversals, indicated by crosses, in these characters; B. Common ancestor possesses the primitive states of characters 8 and 38, and the derived states are acquired independently in *Genyophryne* and the Asterophryinae except *Barygenys*, which possesses the primitive states.

ligamentous connexion of the maxillae (38). If *Genyophryne* and the Asterophryinae form a monophyletic group, either their common ancestor had evolved three *Mm. petrohyoidei posteriores*, and extension of and connexion of the partes faciales which subsequently underwent reversal in *Barygenys* (Fig. 29A), or else the common ancestor maintained the genyophrynine condition, and parallel evolution occurred, *Genyophryne* and Asterophryinae except *Barygenys* acquiring the apomorphous states independently (Fig. 29B).

It is necessary to assess the relative likelihood of these two models. The *Mm. petrohyoidei posteriores* of *Barygenys* differ from both the asterophryine and genyophrynine conditions, and have evolved either by loss of the entire *M.p. posterior* II of an asterophryine-like ancestor, or by reduction of the posterior slip of a genyophrynine-like ancestor. As indicated earlier in

the discussion of this character, I can see no reason to favour either hypothesis.

On the other hand, the conformation of the snout of *Barygenys* seems unlikely to have evolved from the condition shared by the asterophryines and *Genyophryne*, as such as evolutionary step would involve the loss by a burrowing animal of one mode of reinforcement of the snout (by extension of the maxillae and their connexion anteriorly to the premaxillae) and acquisition of a radically different mode of reinforcement, involving reduction of the premaxillae, and the buffering of the points of weakness in the snout (the gaps between the bones) by ridges of thickened skin (Fig. 20). Such a course of evolution, from one specialised burrowing conformation to another radically different, seems far less likely than the *de novo* acquisition of the different burrowing adaptations in the different lineages from a generalised genyophrynine- or microhyline-like ancestor.

Thus, while a common ancestor of *Genyophryne*, *Barygenys* and the other asterophyrines possessing the asterophryine condition of three *Mm. petrohyoidei posteriores* may be envisaged, I cannot envisage an ancestor of *Barygenys* possessing the snout conformation shared by *Genyophryne* and the asterophyrines, and I favour the hypothesis that this state evolved convergently (*sensu lato*) in *Genyophryne* and the Asterophryinae, which raises the possibility that the other similarities of *Genyophryne* and the Asterophryinae are likewise convergences.

(ii) Conflict with apparent synapomorphies between other genyophrynines and the asterophryines.

Some characters indicate that if the Asterophryinae indeed evolved from a genyophrynine ancestor, *Cophixalus* rather than *Genophryne* forms the sister group to the Asterophryinae, the position implied by Zweifel (1972) and Tyler (1979), presumably on the grounds that *Cophixalus* and the Asterophryinae share the derived state of a reduced pectoral girdle (43). If a case can be made to establish *Cophixalus* as a possible sister-group of the Asterophryinae, it would decrease the plausibility of the apparent autapomorphies of the group *Genyophryne*-Asterophryinae, and, provided the case for a natural group *Cophixalus*-Asterophryinae were not too compelling, weaken the credibility of the hypothesis that the Asterophryinae evolved from any genyophrynine ancestor.

Two additional characters support the monophyly of *Cophixalus* and the Asterophryinae: overlap of the *Mm. interhyoideus* and *intermandibularis* (2); and complex tongue-surface (50).

The characters supporting *Cophixalus*-Asterophryinae monophyly are not compelling. The pectoral girdle has undergone reduction many times in the Microhylidae and Ranidae, and there is a reasonable likelihood that reduction took place independently in *Cophixalus* and the Asterophryinae from an ancestor

TABLE 5. GROUP SHARING DERIVED CHARACTERS WITH *GENYOPHRYNE*

Group	Character
Barygenys, Xenorhina	32 Broad cultriform process of the parasphenoid (probably derived).
	42 Well-developed crista ventralis of the humerus (probably derived).
Barygenys, Xenorhina, Cophula	47 Small eye.
Asterophrys, Hylophorbus, Pherohapsis, Xenorhina, Mantophryne	37 Otic ramus of the squamosal overlying the crista parotica.
Asterophryinae, Cophixalus pansus	29 Laterally broadened palatine-prevomer.
Asterophrys, Pherohapsis	35 Connection of the zygomatic ramus of the squamosal and the maxillary.
Hylophorbus, Pherohapsis, Mantophryne	26 Parasagittal ridge delimiting the extent of adductor muscles on the frontoparietals.

with the condition exhibited by *Genyophryne*. Moreover, I suggest that as small and juvenile specimens of asterophryines exhibit the genyophrynine states of characters (2) and (50), and only large specimens of *Cophixalus* exhibit the asterophryine states of these characters, these may be states related to degrees of development, rather than states which evolved in a common ancestor shared only by *Cophixalus* and the Asterophryinae.

I conclude that the evidence for *Cophixalus*-Asterophryinae monophyly is too weak to threaten the case for *Genyophryne*-Asterophryinae monophyly.

(iii) Cases of convergence involving *Genyophryne* and members of the Asterophryinae.

There are seven derived states shared by *Genyophryne* and a small number of asterophryines, and sometimes some genyophrynines (Table 5). In many cases the distributions of these states support incompatible natural groups, and the derived states of characters 29 and 47, which would support very odd natural groups, are highly unlikely to have evolved only once.

Importantly, of the 12 characters shared by *Genyophryne* and some or all of the Asterophryinae, eight (characters 26, 29, 32, 33, 34, 35, 37 and 38) relate to the enlarging and reinforcement of bones of the skull, and with two others (42, development of the humerus; and 47, reduced eye size) are likely burrowing adaptations. If these ten characters were reduced to one: "adaptation to a head-first burrowing mode of life", this may better express the relationship between *Genyophryne* and the asterophryines. The two shared derived states (7, loss of a deep slip to the *M. hyoglossus*; and 8, possession of three *Mm. petrohyoidei posteriores*) which are not at least notionally related to the burrowing way of life are states which have evolved independently in the Microhylinae (in *Kaloula* (7) and *Elachistocleis* (8)).

I therefore regard the hypothesis of monophyly of *Genyophryne* and the Asterophryinae, although apparently supported by many characters, only weakly supported when the characters are examined. If the monophyly of this group is only weakly supported, then the hypothesis of the monophyly of the Genyophryninae is not falsified but still an open question.

Hypothesis 3. Monophyly of the genera and suprageneric groups within the Asterophryinae

Having established the monophyly of the Asterophryinae and having discussed its relationship with the Genyophryninae, I now establish the monophyly of groups within the Asterophryinae.

(a) Monophyly of *Barygenys*.

The monophyly of *Barygenys* is supported by the following autapomorphies: posterior supplementary slip of the *M. intermandibularis* from the ventral surface of the angulosplenial to the ventral surface of the *M. genioglossus basalis* (1); lamellate *M. genioglossus basalis* (6); two *Mm. petrohyoidei posteriores*, the posterior of which inserts on the epicondyle of the posteromedial process of the hyoid only (8); insertion of the *M. longissimus dorsi* on the dorsal fascia (14); the *Mm obliqui* and *transversi* of each side meeting on the ventral surface of the abdomen (16); the *M. serratus medius* with only one insertion (17); the *M. opponens hallucis* from the dorsal surface of the plantar aponeurosis (23); the otic ramus of the squamosal overlying the anterior and dorsal surfaces of the otic capsule (37); no overlap of the maxillae anterior to the premaxillae; compression of the premaxillae between the maxillae; possession of three cutaneous ridges of the snout (38).

Barygenys is a very uniform genus and of the above nine character states, none is shared by any other microhylid examined.

(b) Monophyly of *Phrynomantis*.

The monophyly of *Phrynomantis* (including *Phrynomantis doriae*) is supported by two autapomorphies: two supplementary slips to the *M. intermandibularis*, the anterior from a deep tendon, the posterior direct from the dentary (1); and the dorsal surface of the otic ramus of the squamosal continuous with the lateral surface of the squamosal shaft; the medial flange of the shaft reduced (37).

Of these states the first (1) is unique, and the latter is shared only by microhylines with very small otic rami (e.g. *Microhyla*), far smaller than those of *Phrynomantis*.

(c) Monophyly of *Xenobatrachus* and *Xenorhina*.

The monophyly of the group comprising *Xenobatrachus* and *Xenorhina* is supported by the following autapomorphies: the *M. genioglossus basalis* possessing a posterad cultriform projection (6); a major component of the *M. depressor mandibulae* arising on the otic ramus of the squamosal (11); posteromedial projection of the anterior margin of the palatine

process of the maxillary (39); posterior section of the tongue bearing deep longitudinal striae (51).

Of these four autapomorphies, three (6, 39, 51) are states which occur only in these two genera, and though the *M. depressor mandibulae* arises mostly from the otic ramus in *Choerophryne* and the *darlingtoni*-group, the form of the *M. depressor mandibulae* in those taxa is very different, as there is no slip from the dorsal fascia overlying the otic ramus. In subsequent discussion I refer to this pair of genera collectively as the *Xenorhina*-group.

(d) Monophyly of *Asterophrys*, *Hylophorbus*, *Mantophryne* and *Pherohapsis*.

The monophyly of this group is supported by two autapomorphies: distal organ of the *M. tibialis anticus brevis* (22); and large subarticular tubercles (48). A third shared state which is unique among the Asterophryinae and is probably derived is the origin of the *M. geniohyoideus lateralis internus* entirely from the hyale (5).

Several other characters which are derived or probably derived are shared by members of this group: distal separation of the *M. tibialis anticus longus* into bellies (*Asterophrys*, *Hylophorbus* and *Mantophryne*) (21); parasagittal ridges on the frontoparietals (*Hylophorbus*, *Mantophryne* and *Pherohapsis*) (27); exostosed sheet of bone between the squamosal and the maxillary (*Asterophrys*, *Pherohapsis*) (35); posterad projection of the zygomatic ramus of the squamosal (*Asterophrys*, *Pherohapsis*, *Mantophryne lateralis*) (36); type 1 ilio-sacral articulation (*Hylophorbus*, *Pherohapsis*, *Mantophryne infulata* and *M. lateralis*) (46); and wart-like protrusions of the skin of the chin (*Asterophrys*, *Pherohapsis*, *Mantophryne lateralis* and *M. louisiadensis*) (52).

Neither of the autapomorphies of this group (22, 48) occurs in the other microhylids examined. This group's state of the *M. geniohyoideus lateralis internus* is shared by the aberrant *darlingtoni*-group and *Elachistocleis*.

The hypothesis of monophyly of this group is in conflict with the hypothesis of monophyly of *Asterophrys*, *Xenobatrachus* and *Xenorhina*. The latter hypothesis is supported by two apparent autapomorphies: (1) supplementary slips of the *M. intermandibularis* arising from posteriorly on the ventral surface of the angulosplenial; and (12) segmentation of the *M. adductor mandibulae posterior longus*. The ventral origin of the supplementary slips has occurred probably independently in three other Papuan microhylid genera: *Barygenys*, *Genyophryne* and *Sphenophryne*. Segmentation of the *M. adductor mandibulae posterior longus* has probably arisen independently in *Barygenys*. I regard neither of these characters as reliable an indicator of relationships as characters (5), (22) and (48).

I regard *Asterophrys*, *Hylophorbus*, *Mantophryne* and *Pherohapsis* as forming a monophyletic group which has undergone extensive radiation, reflected in

its disposition by Zweifel (1972) into four genera, three of them monotypic. In subsequent discussion in this section this group is referred to as the *Asterophrys*-group, and the taxonomic implications of its monophyly are deferred.

Hypothesis 4. Monophyly of *Phrynomantis*, the *Xenorhina*-group and the *Asterophrys*-group.

In four characters, *Barygenys* alone of the asterophryines exhibits the plesiomorphic condition, and *Phrynomantis*, the *Xenorhina*-group and the *Asterophrys*-group share the apomorphic condition: lack of the *M. geniohyoideus medialis* (4); the *M. lubricalis brevis digiti* IV medial slip (of the manus) a stout muscle arising via a short tendon from the centrale postaxiale (20); distal separation of the *Mm. lumbricales breves digitorum* IV and V of the pes (24); and the lateral margins of the frontoparietals strongly down curved, so that the braincase is relatively narrow (25).

This apparently well-supported hypothesis conflicts with another apparently well-supported hypothesis: the monophyly of a group formed by *Barygenys* and the *Xenorhina*-group. The derived character states shared by these genera are: the *M. adductor mandibulae posterior longus* segmented with a superficial tendon of insertion (12); the *M.a.m. externus superficialis* arising partly from the fascia (13); origin of the *M. levator scapulae inferior* in part from the ventral surfaces of the first three vertebrae (18); a large deep slip of the *M. pectoralis sternalis* (19); mesial expansion of the vomero-palatine well developed (30); and reduction in the number of denticles on the posterior palatal fold (53).

In addition to the shared and derived states exclusive to this group, a number of other states which are probably derived are shared also by other non-asterophryine taxa: cultriform process of the parasphenoid broad (*Genyophryne*) (32); crista ventralis of the humerus well developed (*Genyophryne, Elachistocleis, Glyphoglossus* and *Kaloula*) (42); and eyes small (*Copiula* and *Genyophryne*) (47).

Despite the preponderance of apparent autapomorphies supporting the concept of *Barygenys-Xenorhina*-group monophyly, and falsifying the hypothesis of *Phrynomantis- Xenorhina*-group *Asterophrys*-group monophyly, the latter hypothesis is preferable for the following reasons.

(a) The monophyly of *Barygenys* and the *Xenorhina*-group implies that the sister-group of *Barygenys* and the *Xenorhina*-group is either *Phrynomantis*, the *Asterophrys*-group, or a hypothetical common ancestor of those two groups (Fig. 30). Therefore the hypothetical ancestor of *Barygenys* and the *Xenorhina*-group would be postulated to possess the states of characters 4, 20, 24 and 25 possessed by the *Xenorhina*-group and the other asterophryines, and the states possessed by *Barygenys* (*M. geniohyoideus medialis* present; genyophrynine-like conditions of the *M.*
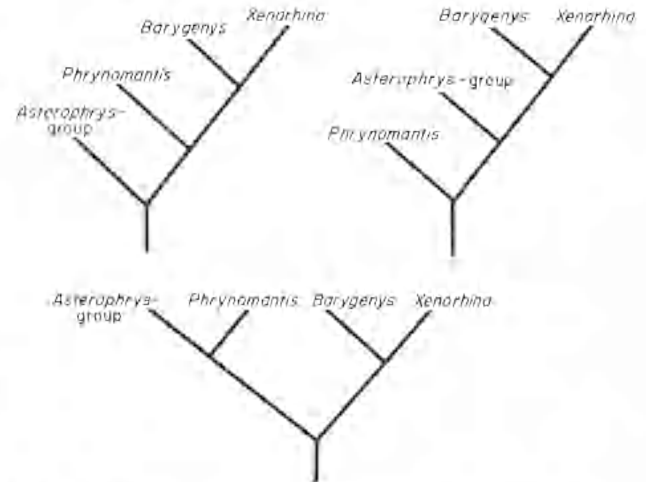

FIG. 30. Possible cladograms of the Asterophryinae, assuming *Barygenys-Xenorhina* group monophyly.

lumbricalis brevis IV of the manus and *Mm. lubricales breves* IV and V of the pes; broad, relatively flat frontoparietals) to be reversals to the genyophrynine condition. The implications of this are:

(i) *Barygenys* must have reacquired a muscle, the *M. geniohyoideus medialis* (4) not present in its ancestral species. While this is possible, it is less likely than the situation in which a common ancestor of *Barygenys* and the other asterophryines possessed the muscle, and that it subsequently was lost in the ancestor of the other asterophryines but retained in *Barygenys*.

(ii) The Asterophryines are all either terrestrial or fossorial, whereas the genyophrynines occupy a variety of niches: scansorial, terrestrial, fossorial and aquatic. The reversion of the specialised fossorial *Barygenys* to the generalised condition of hand and foot musculature of the diverse genyophrynines (20, 24) appears unlikely.

(iii) As has been discussed above, the loss of maxillary extension and connexion and acquisition of a radically different mode of adaptation of the snout to burrowing, as are implied by the postulated common ancestry of *Barygenys* and the *Xenorhina*-group, appear unlikely evolutionary events.

(b) Of the nine shared and derived characters supporting the hypothesis of monophyly of *Barygenys* and the *Xenorhina*-group, three relate to the strengthening of the arm action (18, 19, 42), two to the reinforcement of the skull (30, 32), and two to the reduction of size of the eye (13, 47). These all relate, at least notionally, to the burrowing habit. The arm action of *Barygenys* when walking is extreme (as the forearm is pulled through about 180°, from the vicinity of the eye to the flank — personal observation). The arms are involved in pulling *Barygenys* through the moss and leaf litter, and Characters 18, 19 and 42 appear to relate to this action. Acquisition of a similar mode of burrowing in the *Xenorhina*-group, of which I did not observe living specimens, would be expected to lead to similar adaptations. That three of these shared character states (32, 42, 47) occur in unrelated

fossorial species indicates the possibility of convergent acquisition of these states in the two fossorial genera of asterophryines also.

(c) While differences in characters do not indicate distance of relationship, I accept Arnold's (1981) argument that evolution in two taxa of different solutions to common problems is indirect evidence that the taxa may be distant. As well as differences in the mode of reinforcement of the premaxillary region, *Barygenys* and the *Xenorhina*-group differ in some other forms of skull reinforcement: in *Barygenys* alone, there is a calcified arc between the septomaxillaries (4), in the *Xenorhina*-group alone the anterior margins of the palatine shelves of the maxillae project postero-mesially towards the anterad process of the vomer-palatine (39).

(d) The *Asterophrys*-group and the *Xenorhina*-group share a derived state, possession of a dorsal crest of the ilium (45). This state, which does not occur in other microhylids is an apparent autapomorphy supporting the hypothesis of monophyly of the *Asterophrys*-group and the *Xenorhina*-group, which is incompatible with *Barygenys-Xenorhina*-group monophyly.

The evidence, therefore, favours the hypothesis that *Phrynomantis*, the *Xenorhina*-group and the *Astero-phrys*-group form a natural group, and that *Barygenys* and the *Xenorhina*-group do not.

Hypothesis 5. Monophyly of the *Xenorhina*-group and the *Asterophrys*-group.

The solution of the three-taxon problem of relation-ships between *Asterophrys*-group, *Phrynomantis* and the *Xenorhina*-group is modified by the establishment of *Barygenys* as the sister-group of the three taxa. However, the estimation of polarities of character states is not made easier. As the states of character (10), (12), (13), (18), (19), (30), (32), (42), (47) and (53) exhibited by *Barygenys* conflict with those exhibited by the genyophrynines, the fact that *Barygenys* joins the Genyophryninae in the role of out-group to the three taxa simply obscures the polarities of these characters.

The only unequivocal autapomorphy supporting the monophyly of the *Xenorhina*-group and the *Astero-phrys*-group is the possession of the ilial crest (45). Another shared and probably derived character is the

FIG. 31. Cladogram of the groups of asterophryines.

extension of the otic ramus medially to overlie the crista parotica (37). This state is shared by *Genyophryne*, and a similar but not identical extension is seen also in *Choerophryne* and the *darlingtoni*-group. This state has been subject to convergence and is not a reliable indicator of relationships.

This hypothesis of monophyly is in conflict with the hypotheses that *Phrynomantis* and the *Xenorhina*-group form a natural group, for which there is no evidence, and that the *Asterophrys*-group and *Phrynomantis* form a natural group, which I now consider.

Hypothesis 6. Monophyly of *Phrynomantis* and the *Asterophrys*-group.

This hypothesis is supported by one apparent autapomorphy: origin of the *M. petrohyoideus posterior* 111 from the zygomatic ramus or its posterad projection (9). This state occurs also in *Elachistocleis*.

There appears to be no way of deciding between the hypotheses 5 and 6 of monophyly presented here. Both characters (45) supporting monophyly of the *Xenorhina*-group and the *Asterophrys*-group and (9) supporting monophyly of the *Xenorhina*-group and *Phrynomantis* appear equally valid. Given the present state of knowledge, the best course appears to be to admit that the relationship between the three groups is unresolved, and best expressed on a cladogram as a trichotomy (Fig. 31).

Phylogeny of the *Asterophrys*-group. Here I attempt to establish a phylogeny of the *Asterophrys*-group. This exercise is undertaken on the assumption that the *Asterophrys*-group is monophyletic (*sensu* Hennig, 1966), i.e., that this group comprises all of the descendants of a common ancestor. *Phrynomantis kopsteini* was unavailable for dissection (only three specimens are known), and as this may well be a member of the *Asterophrys*-group, conclusions concerning the phylogeny of this group can only be conditional. Evidence that *P. kopsteini* is a member of the *Asterophrys*-group is that (1) the "subarticular tubercles are strong" (Zweifel 1972, p. 479: *contra* Mertens, 1930), and (b) "the anterior process of the maxillae are only narrowly separated at the midline, so the condition is virtually symphygnathine" (Zweifel 1972, p. 479). This condition of the maxillae appears similar to that of *Mantophryne infulata*, in which the maxillae are separated by between 0.2 and 0.3 mm in the three specimens available.

As has been pointed out above, the *Asterophrys*-group is very diverse, and within this group relation-ships are obscure. Conflicting trends occur, e.g., towards exostosis of the skull — none in *Hylophorbus* and *Mantophryne infulata*, slight in *M. louisiadensis*, moderate in *M. lateralis*, heavy in *Asterophrys* and *Pherohapsis* — and towards lightening of the skull, expressed in the lack of symphygnathy in *Hylophorbus* and the marginal symphygnathy of *M. infulata*. Moreover, in a phylogenetic analysis, "trends" are
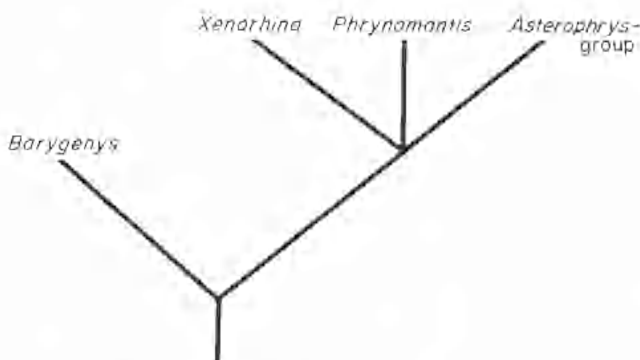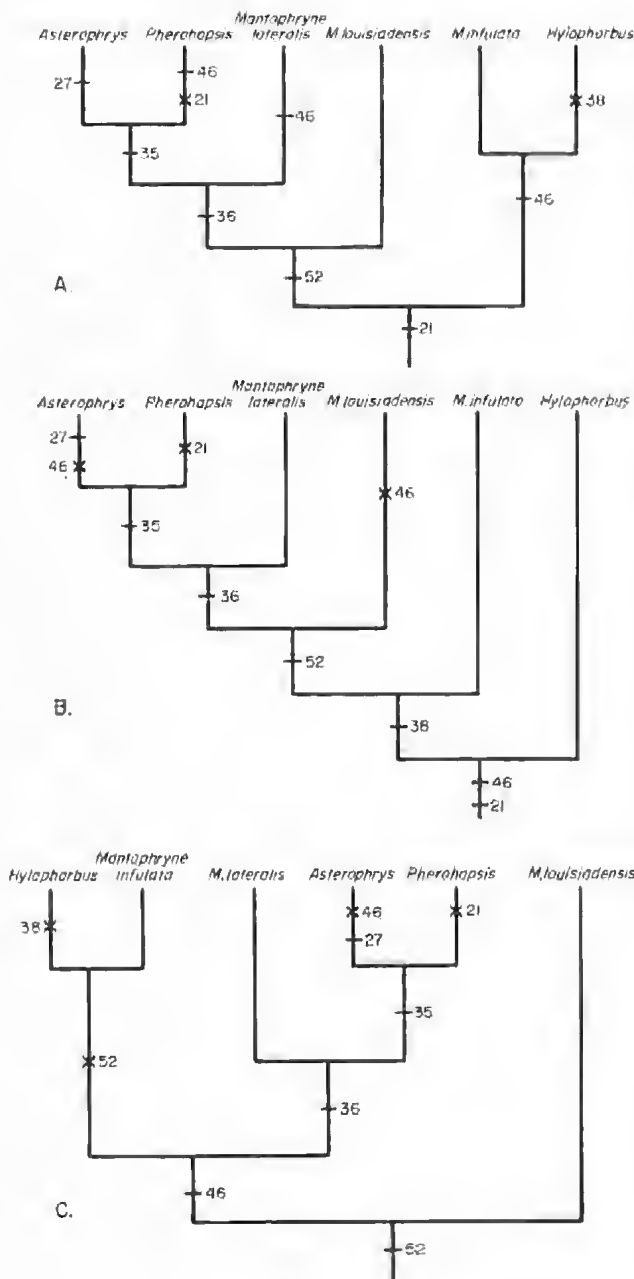
FIG. 32. Three of the most parsimonious cladograms of the *Asterophrys*-group produced by the WISS method. Horizontal strokes through lines indicate acquisition of a derived character state; crosses indicate reversals. Several cladograms as parsimonious as (B) can be produced with different treatments of character 46.

uninformative unless shared, derived character states can be identified.

The establishment of character state polarities is also complicated by uncertainty as to the appropriate sister-group of the *Asterophrys*-group (Fig. 30), resulting from any inability to resolve the *Phrynomantis-Xenorhina*-group-*Asterophrys*-group trichotomy. The sister-group, the most appropriate functional outgroup for this group of species, could be *Barygenys* or the *Xenorhina*-group or *Phrynomantis*, depending on how the trichotomy were resolved. Consequently, only six characters potentially informative of relationships in this group can be assigned polarities, and the polarity of Character 38, symphygnathy of the upper jaw, is
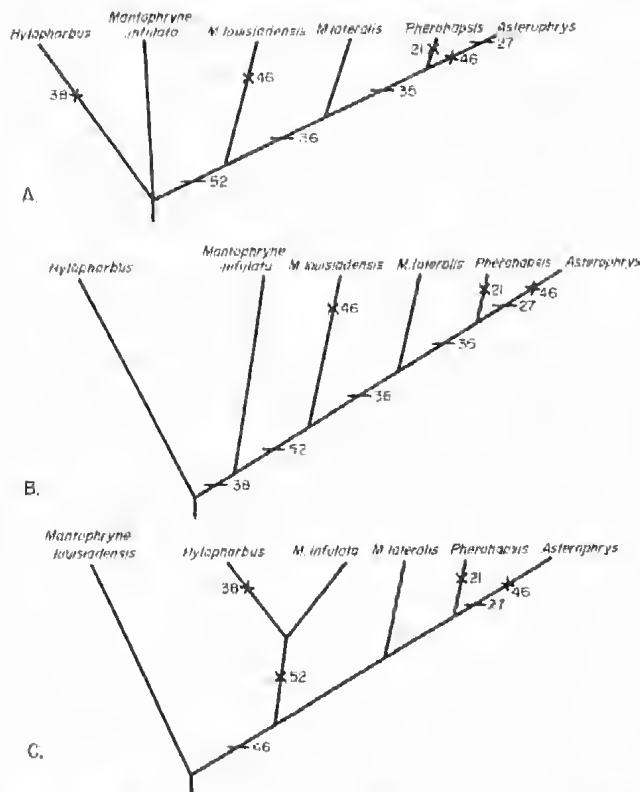
TABLE 6. CHARACTER STATES OF THE *ASTEROPHRYS*-GROUP

Species	Character						
	21	27	35	36	38	46	52
Asterophrys turpicula	1	A[1]	1	1	A[2]	0	1
Hylophorbus rufescens	1	B	0	0	B	1	0
Pherohapsis menziesi	0	B	1	1	A	1	1
Mantophryne infulata	1	B	0	0	A	1	0
M. lateralis	1	B	0	1	A	1	1
M. louisiadensis	1	B	0	0	A	0	1

[1] The relationship between the sagittal crest of *Asterophrys* and the parasagittal ridges of other species is unknown.
[2] As there is conflict in the information from the outgroup, polarities cannot be assigned.

unknown. On the other hand, the polarity of Character 46 is resolved, type I ilio-sacral articulation being the derived state. The polarities are listed in Table 6.

The other characters given conflicting evidence of relationship: Character 21 (division of the *M. tibialis anticus longus*) supports the monophyly of *Asterophrys, Hylophorbus* and *Mantophryne;* Character 35 (connexion between the squamosal and maxilla) supports the monophyly of *Asterophrys* and *Pherohapsis*, Character 36 (posterad projection of the zygomatic ramus) supports the monophyly of *Asterophrys, Pherohapsis* and *Mantophryne lateralis*; Character 46 (nature of the iliosacral articulation) supports the monophyly of *Hylophorbus, Pherohapsis, Mantophryne infulata* and *M. lateralis*; and Character 52 (chin warts) supports the monophyly of *Asterophrys, Pherohapsis, Mantophryne lateralis* and *M. louisiadensis*. There is no reason to believe that any of these characters is more reliable than the others: the derived states of Characters 35 and 46 have evolved convergently within the Genyophryninae; the homology of the prootic arcade of *Pherohapsis* with the posterad process of *Asterophrys* and *Mantophryne lateralis* (36) is unproven (Introduction); and Character 21 may well be related in this group to the relative length of the tibiofibula, which is relatively less in *Pherohapsis* than in other members of the *Asterophrys*-group, and is variable within genera (Zweifel 1972). In order to illustrate graphically the possible relationships Figs 32-34 show the most parsimonious cladograms constructed by the Weighted Invariant Step Strategy of Farris, Kluge and Eckhardt (1970) (Fig. 32), the Wagner Tree method of Lundberg (1972) (Fig. 33) and a phylogenetic tree constructed by the Character Compatibility Analysis method of Meacham (1981) (Fig. 34). These demonstrate the ambiguities arising from the uncertain polarity of Character 38 (cf. Figs A and B of each Figure) and from the paucity of characters. However, I conclude from these figures the following:

(i) Monophyly of the groups *Asterophrys-Pherohapsis* and *Asterophrys-Pherohapsis-Mantophryne lateralis* appear to be best supported by the data.

(ii) No support is given to the hypothesis of the monophyly of *Mantophryne*. *M. lateralis* appears to be related to *Pherohapsis* and *Asterophrys*, the

FIG. 33. Three of the most parsimonious cladograms of the Asterophrys-group produced by Lundberg's (1972) method.

FIG. 34. Two of the most parsimonious cladograms of the Asterophrys-group produced by the Character Compatibility Analysis method.

relationships of *M. louisiadensis* are obscure, and the close phenetic relationship *M. infulata* bears to *Hylophorbus* may or may not be the result of symplesiomorphy.

(iii) Parallel acquisition of the type 1 ilio-sacral articulation by *Hylophorbus, Pherohapsis, M. infulata* and *M. lateralis* and parallel reversal to the type IIA articulation by *Asterophrys* and *M. louisiadensis* are equally parsimonious hypotheses.

It is clear that the data are insufficient for many confident statements to be made about relationships within this group.

Hypothesis 7. Monophyly of *Xenorhina* and *Xenobatrachus*

The one feature distinguishing these genera is the occurrence in *Xenobatrachus* of the derived state of Character (31), presence of one or more spike-like odontoids on the vomero-palatine. I conclude that *Xenorhina* is paraphyletic and *Xenobatrachus* arose from a Xenorhina-like ancestor.

DISCUSSION

Taxonomic Implications of the Phylogenetic Analysis

Some of the data presented in this study point inescapably to the necessity for taxonomic changes which involve redefinition of the asterophryine genera. The changes to be made will involve decisions related to the philosophy of classification.

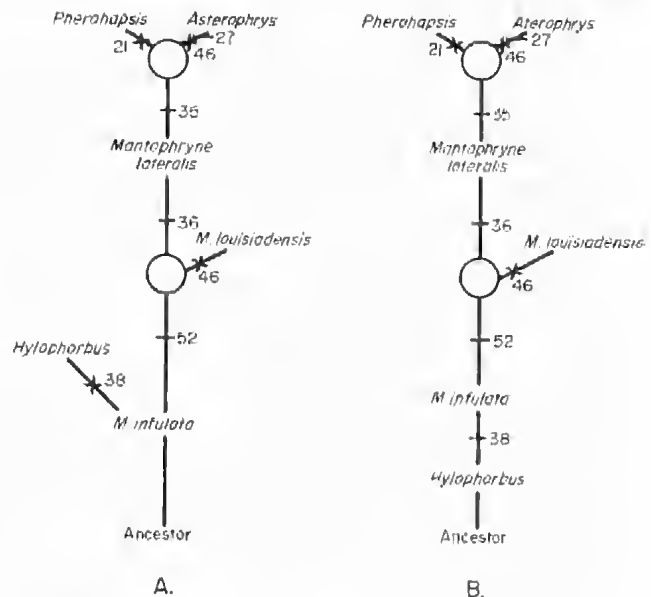Few would disagree that a classification should be useful. Yapp (1981, p. 245) encapsulated the functions

and properties of a useful classification: "The fundamental object of classification is to facilitate economical statements. If we can agree that bats, cats and rats are mammals, we say, 'Mammals have hair,' instead of 'Bats ... cats ... rats have hair,' and if a newly discovered kangaroo is a mammal, it too has hair. A secondary value is to enable a museum curator to put his specimens in appropriate cupboards." Yapp implies that whatever its basis, a classification must establish "groupings about which generalizations can be made" (Mayr 1981, p. 511), and so have maximal predictive value, and, because its information content is high, be stable in the face of new information.

Each of three schools of classification, the phenetic (e.g., Sneath and Sokal 1973) the evolutionary (e.g., Mayr 1969; Michener 1978; Mayr 1981) and the cladistic (e.g., Farris 1977; Eldredge and Cracraft 1980) claims to incorporate maximum information content and predictive value into its classifications. Each claims to seek out "natural groups". However, the meaning of "natural group" differs between the schools. Pheneticists define natural groups as groups based on overall similarity (Sneath and Sokal 1973, p. 24); evolutionists define natural groups as groups sharing greatest genetic similarity (Mayr 1969); and cladists define natural groups as monophyletic (*sensu* Hennig 1966) or as groups sharing particular defining characters (Nelson and Platnick 1981, p. 328). In the recognition of natural groups, cladistic relationship is either irrelevant,

"... this measure of similarity does not carry with it any necessary implication as to the relationship by ancestry, but does imply exhaustive estimates of similarity of the phenotypes." (Sneath and Sokal 1973, p. 28)

relevant, but not the whole story,

"... a relationship, in the evolutionary sense is determined by

both processes of phylogeny, namely, branching and subsequent divergence." (Mayr 1969, p. 70)

or all,

"The prime goal of systematics, according to cladists, is the definition and recognition of monophyletic groups." (Eldredge and Cracraft 1980, p. 10)

The schools are not monolithic. For example, Holmes (1980) reviewed the diversity of the evolutionary school, and well publicised differences of opinion occur between practitioners of transformed cladistics (i.e., cladistics divorced from evolutionary theory, e.g., Platnick 1980; Patterson 1980; Nelson and Platnick 1981) and Hennigian phylogeneticists, who relate phylogenetic patterns to evolution (e.g., Eldredge and Cracraft 1980; Ball 1981; Wiley 1981; Beatty 1982). However, though not monolithic, the schools are well delineated, and a systematist revising and redefining taxonomic groups must either knowingly or unknowingly follow the tenets of one of the schools.

The phenetic school claims that the most useful, objective and stable classification arises out of an analysis of as large a selection of characters as possible, in order to gain a measure of overall similarity, without reference to the evolution of the taxa. The stability of phenetic classifications has been thrown into doubt by the studies of Mickevich and Johnson (1976) Mickevich (1978) and Schuh and Polhemus (1980).

It has long been known that different clustering methods to discover groups of most similar taxa produce different results, and this has been demonstrated conclusively by Presch (1979). Though Sneath and Sokal (1973, p. 31) saw a virtue in this divergence:

". . . some types of differences in results may themselves be of great interest leading to new insights into the nature of the organisms or of the taxa being studied".

in practice different results from different cluster techniques appear rather to cause confusion. For example, Blake (1973, p. 123) in his revision of the myobatrachine frogs simply rejected the results of one of his two clustering methods on the grounds that it yielded results "inconsistent with other [unspecified] indicators of relationship"; Key (1976, p. 28), lacking "any convincing ground of principle" for choosing between eight different classifications derived from the same data by eight clustering techniques, adopted the previously recognised species-groups as the basis for his classification of the morabine grasshoppers. When such actions are taken it is difficult to accept the efficacy of phenetic classifications.

Some studies, notably that of Blackith and Blackith (1967) on orthopteroids, demonstrated concordance in classifications based on phylogenetic and phenetic methods. However, though they attribute this concordance to their use of a large number of characters, it appears more likely to be the result of the high taxonomic level at which this study was carried out. The study of Schuh and Polhemus (1980) on the Leptopodomorpha indicate that at lower taxonomic

levels agreement between the results of phylogenetic and phenetic methods is low.

Pheneticists sacrifice the information content of phylogeny for objectivity and stability. On both counts phenetic techniques appear to fail, as groups claimed to be natural because they are based on overall similarity must be chosen by a subjectively chosen technique, and appear to be susceptible to change if new information is added. The sense in which such a group can be said to be natural is obscure.

The other two schools utilize phylogenetic data, but differ in that the classifications of evolutionists incorporate anagenetic information, as they claim that this action increases the information content and predictivity of their classifications, a claim disputed by Farris (1977). At the heart of the dispute between these schools is the treatment of paraphyletic groups. Evolutionists, e.g., Ashlock (1971, 1974), Mayr (1974), Brothers (1975), Bock (1977) and Michener (1977, 1978), consider paraphyletic groups natural and worthy of recognition; phylogeneticists and "transformed" cladists, e.g., Hennig (1975), Nelson (1978), Eldredge and Cracraft (1980), Nelson and Platnick (1981) and Wiley (1979, 1981) consider only monophyletic (*sensu* Hennig) groups natural.

The arguments of both sides to this question appear to have merit. It is argued by evolutionists that if it is assumed that, for example, fleas evolved from a fly species and therefore, flies are paraphyletic (Michener 1978), a name is needed for fleas and flies to distinguish them, as useful generalizations can be made about each group. Mayr (1974) argues also that paraphyletic groups may be considered natural if they have retained morphological similarities owing to their fidelity to an adaptive zone (e.g. the reptiles), because this morphological similarity may be assumed to be the result of genetic similarity, and it is the relative genetic uniformity of a group that makes it natural.

Against this view it is argued that paraphyletic groups such as the flies do not necessarily represent a group of most closely related species: among the flies there is a sister-group to the fleas. That group of flies is more closely related to the fleas than to the other flies, and therefore paraphyletic groups should not be considered natural: they are defined simply by lack of the autapomorphies of the fleas. Indeed the assumption that retained morphological similarity is necessarily related to a retained genetic similarity is questionable. Patterson (1981a) cites the study of Bruce and Ayala (1979) to show that, despite their morphological similarity to *Pongo*, the African apes, a paraphyletic group with the taxonomic removal of man, are genetically far closer to man than to *Pongo*; and Patterson shows that carp, a member of the paraphyletic Osteichthyes, are much closer genetically to man and to chickens, to which they are phylogenetically closer, than to sharks which they resemble morphologically. As assumed genetic affinity is the basis for

belief in the naturalness of paraphyletic groups, evolutionary classifications are of dubious value.

The demonstrated stability of cladistic classifications (Mickevich 1978; Schuh and Polhemus 1980), the necessity of cladistic classifications in some methods of historical biogeography (Brundin 1966, 1968; Rosen 1978; Patterson 1981b), their high information content (Farris 1977), and the unanimous belief of evolutionists and phylogeneticists that monophyletic groups are natural, suggest the desirability of adopting a phylogenetic classification. However, as I pointed out above, paraphyletic groups, to the extent that they are useful, i.e., to the extent that useful generalizations can be made about them, need to be recognized.

The Annotated Linnean Hierarchy of Wiley (1979, 1981) is based on only monophyletic groups, but can accommodate paraphyletic and polyphletic groups, and also groups of unknown affinities. It appears to offer the kind of compromise that is needed. In Wiley's scheme, taxa forming an asymmetrical part of a phylogenetic tree may be placed at the same categorical rank and sequenced in their phylogenetic order of origin, thereby relaxing the Hennigian requirement of a separate taxonomic rank for every fork of such a tree. Trichotomies are recognized by the term "sedis mutabilis" to indicate the sequence of the three taxa in the hierarchy is interchangeable. Groups that are paraphyletic, polyphyletic or of unknown status are denied formal rank, and are labelled by inverted commas and the term "incertae sedis". As the Annotated Linnean Hierarchy appears to offer a phylogenetic classification that has the capacity to incorporate additional useful anagenetic information without loss of rigour, I use it in this revision of asterophryine taxonomy, with the modification that as the genus is a mandatory category, the paraphyletic genera, though labelled as such in the hierarchy, have formal rank.

Taxonomic Recommendations

A. Genyophryninae

The monophyly of the Genyophryninae has not been demonstrated. Nor has its paraphyly. The status of this subfamily must await a phylogenetic analysis of the subfamilies of the Microhylidae, and the action of amalgamating the Genyophryninae and the Asterophryinae would be premature.

B. Phrynomantis doriae

Phrynomantis doriae lacks the autapomorphies of the *Xenorhina*-group: the supplementary slips of the *M. intermandibularis* arising from the angulosplenial; the cultriform process of the *M. genioglossus basalis*; the striated tongue; and the posteromedial expansion of the anterior corner of the palatine process of the maxillary. It also lacks many other derived states shared

by *Xenorhina* and other genera (Characters 1, 13, 18, 19, 30, 47, 53).

P. doriae possesses the autapomorphies of *Phrynomantis*: the two supplementary slips to the *M. intermandibularis*, the anterior from a deep tendon, the posterior direct from the dentary; and the medial flange of the squamosal shaft reduced, the dorsal surface of the otic ramus instead continuous with the lateral surface of the shaft.

Therefore, I recommend that *Xenorhina doriae* be transferred to the genus *Phrynomantis*, as *P. doriae* (Boulenger).

C. Xenorhina and Xenobatrachus

Xenorhina is paraphyletic, differing from *Xenobatrachus* only in lacking one or more large odontoids on the vomero-palatine. There appear to be two taxonomic options: *Xenobatrachus* could be referred to the synonomy of *Xenorhina* Peters (which has priority); or the genera retain their identities with *Xenorhina* annotated to indicate its paraphyly.

The advantage of the first course is the elimination of the *Xenorhina-Xenobatrachus* dichotomy with its unfortunate concomitant, the obliteration of the relationships of the throat muscles when the diagnostic odontoids are sought. The advantages of the second course are that current nomenclature is conserved; and the identities of two monophyletic groups, *Xenobatrachus* and the *Xenorhina*-group are expressed. As the second course appears to produce a more informative classification, I adopt it.

D. Mantophryne

The three species *Mantophryne infulata*, *M. lateralis* and *M. louisiadensis* show affinities to the *Asterophrys*-group rather than to *Phrynomantis*. When these species are removed, *Phrynomantis* becomes a much more homogeneous genus supported by the autopomorphies listed in the preceding discussion of *P. doriae*. The derived characters shared by these three species with other members of the *Asterophrys*-group are: distal origin of the *M. tibialis anticus brevis* (22); crested ilium (45); large subarticular tubercles (48); and the possible apomorphy: origin of the *M. geniohyoideus lateralis internus* entirely from the hyale (5). It is therefore appropriate to remove these species from *Phrynomantis*. I recommend resurrection of *Mantophryne* Boulenger 1897, type species *M. lateralis*, to accommodate the three species, as there are no compelling data to associate any of the species with any of the existing *Asterophryne*-group genera. No autopomorphy of *Mantophryne* was found, so its monophyly is uncertain. The status of this genus is discussed further in the next section.

E. The Asterophrys-group

The *Asterophrys*-group comprises three divergent monotypic genera (*Asterophrys*, *Hylophorbus* and *Pherohapsis*) and *Mantophryne*, which is a group of uncertain affinities and uncertain monophyly.

Although *Hylophorbus* is phenotypically distinctive, the polarity of its one defining generic character (38: separated maxillae) is dubious, and thus its status as a genus is dubious. The taxonomic choice lies between (a) inclusion of the six species into a single genus (*Asterophrys*) and (b) retention of *Asterophrys* and *Pherohapsis*, resurrecting *Mantophryne* Boulenger 1897 to accommodate three of the species, and regarding *Hylophorbus* and *Mantophryne* as "*incertae sedis*", i.e., paraphyletic or of uncertain monophyly, and "*sedis mutabilis*", i.e., of doubtful order of arising.

I adopt the latter course of action because (a) it conserves much of the current classification; (b) as the species of this group are very divergent, a single generic name would be of little heuristic value; and (c) the monophyly of the entire group and the uncertainty of the status of *Hylophorbus* and *Mantophryne* are expressed.

The convention of placing sister-groups on the same rank necessitates the insertion of a rank intermediate between the subfamily and the genus, which have traditionally been the only ranks between the family and the species in the Microhylidae. I follow Parker (1940) and Lynch (1971) who use the tribe as an intermediate rank in the Leptodactylidae.

The classification I favour is:

FAMILY: MICROHYLIDAE
  SUBFAMILY: Asterophryinae
    TRIBE: Barygenyini
      GENUS: *Barygenys*
    TRIBE: Asterophryini *sedis mutabilis*
      Asterophryini *incertae sedis* "*Hylo phorbus*" *sedis mutabilis*
      Asterophryini *incertae sedis* "*Manto phryne*" *sedis mutabilis*
      GENUS: *Asterophrys*
      GENUS: *Pherohapsis*
    TRIBE: Phrynomantini *sedi mutabilis*
      GENUS: *Phrynomantis*
    TRIBE: Xenorhinini *sedis mutabilis*
      Xenorhinini *incertae sedis* "*Xenorhina*"
      GENUS: *Xenobatrachus*

F. *Phrynomantis h. humicola* and *P.h. compta*

In distinguishing these subspecies, Zweifel (1972) stressed two features: occurrence of a pale orange postocular stripe in *P.h. compta* (lacking in *P.h. humicola*); and possession by *P.h. humicola* of relatively longer legs than those of *P.h. compta*. According to Zweifel's data the ranges of these taxa are essentially allopatric: *P.h. compta* is a western form with its range centring on the Madang and Western Highlands Province, and extending eastwards into Chimbu Province; *P.h. humicola* is an eastern form with its range centring on the Eastern Highlands Province and extending westwards into Chimbu Province. Zweifel (1972) reported one case of sympatry at Igindi, Chimbu Province, but was unwilling to name

P.h. humicola and *P.h. compta* as separate species until evidence of reproductive isolation was available, as the two taxa are very similar morphologically.

These two taxa differ anatomically in two respects: (a) *P.h. compta* possesses a slip of the *M. depressor mandibulae* arising from the posterior margin of the tympanic ring. *P.h. humicola* and some *Barygenys* species are the only asterophryines to lack this slip. (b) In *P.h. compta* the mandibular branch of the trigeminal nerve passes anterolaterally between the *Mm. adductores mandibulae posterior longus* and *anterior longus*. It passes laterally around the anterior margin of the *M.a.m. posterior longus* and posteroventrally across the lateral surface of that muscle until the nerve reaches the mandible. *P.h. humicola* is the only asterophryine which does not conform to this pattern. Instead the nerve passes directly lateroventrally from the braincase, penetrating the *M.a.m. posterior longus*. It emerges on the lateral surface of the *M.a.m. posterior longus* close to that muscle's insertion on the mandible, and passes ventrally on the lateral surface of the muscle until it reaches the mandible.

The specimens examined are from allopatric sites. Examination of sympatric specimens could provide evidence of introgression or genetic isolation.

Systematic Accounts

ASTEROPHRYINAE (part.) Parker, 1934
  Asterophryinae Zweifel, 1971
  Asterophryidae Günther (1858) p. 51
  Xenorhinidae Mivart (1869) p. 289
  Symphygnathinae and Eleutherognathinae (part.) Mehely (1901) pp. 172-189
  Cacopinae (part.) Noble (1931) p. 531

Diagnostic definition: (2) posteromedially directed dorsal sheet of fibres on *M. intermandibularis* lacking; (3) overlap of *Mm. interhyoideus* and *intermandibularis* (except *Xenorhina bouwensi*); (7) deep slip of *M. hyoglossus* to hyoid lacking; (15) three tendinous inscriptions of *M. rectus abdominis*; (28), (29) palatine and vomer fused and expanded both laterally and mesially where each combined bone meets its fellow; (33) broad contact of medial ramus of pterygoid with prootic; (34) broad contact of quadratojugal with maxilla; (41) dentary fused to anterior surface of mentomeckelian and usually in contact anteriorly with its fellow (except *Hylophorbus*), mentomeckelians in contact at an acute angle; (43) pectoral girdle lacking clavicles, procoracoids and omosternum; (44) vertebral column diplasiocoelous; (49), (50) tongue adherent and divided superficially into anterior and posterior sections; (54) larva undergoing metamorphosis in egg capsule, and lacking open gill clefts, operculum and spiracle, respiration performed through non-muscular, vascular tail in known species. Additional states not referred to in previous sections also occur: maxillary and vomerine teeth absent; ear fully developed.

The states of characters (2), (41) and the combination

of the states of (49) and (50) are diagnostic of the Asterophryinae. The Asterophryinae comprises four tribes.

ASTEROPHRYINI New Tribe

This tribe accommodates the genera *Asterophrys, Hylophorbus, Mantophryne* and *Pherohapsis*.

Diagnostic definition: (4) *M. geniohyoideus medialis* absent; (5) *M. geniohyoideus lateralis internus* arising from hyale only; (6) *M. genioglossus basalis* labiform; (8) three *Mm. petrohyoidei posteriores;* (9) *M. petrohyoideus posterior* III arising from zygomatic ramus of squamosal; (10) *M. depressor mandibulae* not arising from anterior 1/2 of ventral margin of tympanic ring; (11) origin of *M. depressor mandibulae* from otic ramus slender; (12) superficial tendon of *M. adductor mandibulae posterior longus* lacking; (13) *M. adductor mandibulae externus superficialis* arising entirely from zygomatic ramus; (14) *M. longissimus dorsi* not inserting on dorsal fascia; (16) *Mm. transversi abdominis* and *Mm. obliqui abdominis externi* terminating on broad ventral aponeuroses; (17) two sites of insertion of *M. serratus medius;* (18) origin of *M. levator scapulae inferior* partly from first two vertebrae; (19) deep slip to *M. pectoralis sternalis* slender; (20) medial slip of *M. lumbricalis brevis digiti* IV of manus cylindrical, arising from centrale postaxiale; (22) *M. tibialis anticus brevis* arising from distally on tibiofibula; (23) *M. opponens hallucis* arising from a distal tarsale; (24) *Mm. lumbricales breves digitorum* IV and V of pes fused along most of their length; (25) frontoparietals 3× as long as broad; (30) median expansion of vomero-palatine moderate; (32) cultriform process of parasphenoid narrow; (37) dorsal surface of otic ramus of squamosal continuous with anterior surface of medial flange of squamosal shaft; (38) maxillae overlapping premaxillae and connected by ligament or suture, no ridges on snout; (39) mesial expansion of anterior margin of palatine shelf of maxilla lacking; (40) anterior margin of nasal capsule not calcified; (42) humerus relatively straight, crest moderately developed; (45) ilium bearing a moderate dorsal crest; (47) eye large (E: S-V > 0.090); (48) subarticular tubercles large and prominent; (51) surface of posterior section of tongue pitted uniformly; (53) posterior pre-pharangeal fold bearing large number of denticles (rarely fewer than ten).

Of these states, (5), (22) and (48) are diagnostic of the Asterophryini.

GENUS *Asterophrys* TSCHUDI, 1838

Asterophrys Tschudi (1838) p. 82
(type species *Ceratophrys turpicola* Schlegel [1837 (1838-1844)]
Asterophrys (part.), Parker (1934) p. 66
Asterophrys Zweifel (1972) p. 432

Diagnostic definition: (1) two supplementary slips to *M. intermandibularis*, each arising from ventral margin of angulosplenial; (12) *M. adductor mandibulae*

posterior longus divided into segments; (21) *M. tibialis anticus longus* divided distally; (26) parasagittal ridges on frontoparietals lacking; (27) sagittal crest on cranium well developed; (35) squamosal and maxilla meeting in large specimens; (36) posterad extension of zygomatic ramus well developed; (38) maxillae meeting anteriorly; (46) direct ligamentous connection between ilium and sacrum; (52) warts on chin well developed.

The states of (1), (12), (27) and (52) are peculiar to *Asterophrys* among the Asterophryini.

Content: A. *turpicula* (Schlegel).

GENUS *Hylophorbus* MACLEAY 1878

Hylophorbus Macleay (1878) p. 136
(type species *H. rufescens* Macleay)
Mantophryne (part.) Boulenger (1897) p. 12
Metopostira Mehely (1901) p. 239
Hylophorbus Zweifel, 1972

Diagnostic definition: (1) one supplementary slip to *M. intermandibularis* via tendon from deep on angulosplenial; (12) *M. adductor mandibulae posterior longus* unsegmented; (21) *M. tibialis anticus longus* divided distally; (26) parasagittal ridges present; (27) sagittal crest lacking; (35) squamosal and maxilla not meeting; (36) posterad extension of zygomatic ramus a slight flange only; (38) maxillae well separated (about 1 mm) anteriorly; (46) ligamentous connexion between ilium and sacrum lacking; (52) chin warts lacking.

The state of character (38) is peculiar to *Hylophorbus* among the Asterophryini.

Content: There are three subspecies of *Hylophorbus rufescens* Macleay: *H.r. rufescens; H.r. extimus* Zweifel 1972; *H.r. myopicus* Zweifel 1972.

Remarks: This genus may be paraphyletic as the polarity of character (38) is dubious.

GENUS *Mantophryne* BOULENGER 1897

Mantophryne Boulenger (1897) p. 12
(type species *M. lateralis* Boulenger)
Mantophryne Vogt (1911) p. 427
Hylophorbus Fry (1913) p. 48
Asterophrys (part.) Parker (1934) pp. 62, 63
Phrynomantis (part.) Zweifel (1972) pp. 476-479, 480-489

Diagnostic definition: (1) one slip to *M. intermandibularis* via a tendon from deep on angulosplenial; (12) *M. adductor mandibulae posterior longus* unsegmented; (21) *M. tibialis anticus longus* divided distally; (26) parasagittal ridges present or absent; (27) sagittal crest absent; (35) squamosal and maxilla not meeting; (36) posterad projection of zygomatic ramus well or poorly developed; (38) maxillae meeting or only narrowly separated (maximum 0.3 mm) anteriorly; (46) ligamentous connexion between ilium and sacrum present or absent; (52) chin warts present or absent.

Content: M. *infulata* (Zweifel) 1972; *M. lateralis* Boulenger; *M. louisiadensis* (Parker) 1934.

Remarks: This is probably a paraphyletic genus, and its relationships with the other genera of the

Asterophryini are uncertain. It differs from *Hylophorbus* in Character 38, from *Asterophrys* in Characters 1, 12, 27 and 52, and from *Pherohapsis* in Characters 21 and 36. I was not able to examine *Phrynomantis kopsteini* Mertens, which may be closely related to the species which comprise *Mantophryne*.

GENUS *Pherohapsis* ZWEIFEL 1972

Pherohapsis Zweifel (1972) p. 456

(type species *P. menziesi* Zweifel)

Diagnostic definition: (1) one slip to *M. intermandibularis* via tendon from deep on angulosplenial; (21) *M. tibialis anticus longus* divided relatively proximally; (26) parasagittal ridges present; (27) sagittal crest lacking; (35) squamosal and maxilla meeting; (36) posterad extension of zygomatic ramus extended medially to meet frontoparietal to which fused to form prootic arch; (38) maxillae meeting anteriorly; (46) ligamentous connexion between ilium and sacrum lacking; (52) chin warts poorly developed.

The states of characters (21) and (36) are peculiar to *Pherohapsis* among the Asterophryini.

Content: P. menziesi Zweifel.

BARYGENYINI New Tribe

This tribe accommodates the genus *Barygenys*.

Diagnostic definition: (1) two supplementary slips to *M. intermandibularis* from the ventral surface of angulosplenial, posterior inserting on *M. genioglossus basalis* by narrow tendon; (4) *M. geniohyoideus medialis* present or absent; (5) *M. geniohyoideus lateralis internus* arising from mandible only; (6) *M. genioglossus basalis* lamellate; (8) two *Mm. petrohyoidei posteriores*; (9) *M. petrohyoideus posterior* III arising from exoccipital and otic ramus; (10) *M. depressor mandibulae* not arising from anterior 1/2 of ventral margin of tympanic ring; (11) origin of *M. depressor mandibulae* from the otic ramus absent or slender; (12) *M. adductor mandibulae posterior longus:* superficial tendon present; segmented in larger species; (13) anterior origin of *M. adductor mandibulae externus superficialis* from fascia; (14) *M. longissimus dorsi* inserting in part on dorsal fascia; (16) *Mm. transversi abdominis* meeting on ventral abdomen, *Mm. obliqui abdominis externi* meeting on ventral abdomen; (17) only one site of insertion of *M. serratus medius;* (18) origin of *M. levator scapulae inferior* partly from first three vertebrae; (19) deep slip of *M. pectoralis sternalis* well developed; (20) medial slip of *M. lumbricalis brevis digiti* IV of manus a narrow sheet from superficial tendon; (22) *M. tibialis anticus brevis* arising relatively proximally; (23) *M. opponens hallucis* arising from palmar aponeurosis; (24) *Mm. lumbricales breves digitorum* IV and V separated proximally; (25) frontoparietals twice as long as broad; (30) median expansion of vomero-palatine well developed; (32) cultriform process of parasphenoid broad; (37) dorsal surface of otic ramus of squamosal continuous with anterior surface of medial flange of squamosal shaft,

and overlying anterior surface of prootic as well as dorsal surface; (38) premaxillae compressed between maxillae; maxillae not meeting; three vertical, dermal ridges on snout; (39) mesial expansion of anterior margin of palatine shelf of maxilla lacking; (40) anterior margin of nasal capsule calcified; (42) humerus curved, crest well developed; (45) ilial crest lacking; (46) direct ligamentous attachment between ilium and sacrum; (47) eye small (E: S-V < 0.090); (48) subarticular tubercles absent or poorly developed; (51) surface of posterior part of tongue pitted uniformly; (53) posterior pre-pharyngeal fold with < 10 denticles.

Of these states, (1), (4), (6), (8), (14), (16), (17), (20), (23), (24), (25), (37), (38) and (40) are peculiar to *Barygenyini* among the Asterophryinae.

GENUS *Barygenys* PARKER 1936

Barygenys Parker (1936) p. 73

(type species *B. cheesmanae* Parker)

Baragenys [sic] Zweifel (1956) p. 9

Diagnostic definition: As above for the tribe Barygenyini.

Content: B. atra (Gunther), 1896; *B. cheesmanae* Parker, 1936; *B. exsul* Zweifel, 1963; *B. flavigularis* Zweifel, 1972; *B. maculata* Menzies and Tyler, 1977; *B. nana* Zweifel, 1972.

Remarks: A new species from Mt Missim is being described (Allison and Burton, *in prep.*).

PHRYNOMANTINI New Tribe

This tribe accommodates the genus *Phrynomantis*.

Diagnostic definition: (1) two slips to *M. intermandibularis*, anterior via narrow tendon, posterior direct from dentary; (4) *M. geniohyoideus medialis* absent; (5) *M. geniohyoideus lateralis internus* arising from both mandible and hyale; (6) *M. genioglossus basalis labiform;* (8) three *Mm. petrohyoidei posteriores;* (9) *M. petrohyoideus posterior* III from zygomatic ramus; (10) *M. depressor mandibulae* with origin usually from entire ventral margin of tympanic ring, rarely posterior 1/2; (11) origin of *M. depressor mandibulae* from otic ramus slender or moderate; (12) *M. adductor mandibulae posterior longus* unsegmented; (13) anterior origin of *M adductor mandibulae externus superficialis* entirely from zygomatic ramus; (14) *M. longissimus dorsi* not inserting on dorsal fascia; (16) *Mm. transversi abdominis* and *obliqui abdominis externi* terminating on ventral abdominal aponeuroses; (17) two sites of insertion of *M. serratus medius;* (18) origin of *M. levator scapulae inferior* partly from first two vertebrae; (19) deep slip of *M. pectoralis sternalis* poorly developed; (20) medial slip of *M. lumbricalis brevis digiti* IV of manus cylindrical, arising from centrale postaxiale; (22) *M. tibialis anticus brevis* arising relatively proximally; (23) *M. opponens hallucis* arising from a distal tarsale; (24) *Mm. lumbricales breves digitorum* IV and V fused along much of length; (25) frontoparietals 3× as long as broad; (30) median expansion of vomero-palatine moderately developed;

(32) cultriform process of parasphenoid narrow; (37) dorsal surface of otic ramus continuous with lateral surface of squamosal shaft, medial flange poorly developed; (38) maxillae meeting anteriorly, no ridges on snout; (39) mesial expansion of anterior margin of palatine shelf of maxilla lacking; (40) anterior margin of nasal capsule not calcified; (42) humerus relatively straight, crest moderately developed; (45) ilial crest lacking; (46) direct ligamentous attachment between ilium and sacrum; (47) eye large (E: S-V > 0.090 usually); (48) subarticular tubercles poorly developed; (51) surface of posterior part of tongue pitted uniformly; (53) posterior pre-pharyngeal fold bearing rarely fewer than ten denticles.

Of these states, (1), (10) and (37) are peculiar to the Phrynomantini among the Asterophryinae.

GENUS *Phrynomantis* PETERS 1867

Phrynomantis Peters (1867) p. 35

(type species by subsequent designation [Noble (1926) p. 20] *P. fusca* Peters).

Callulops Boulenger (1898) p. 345

Gnathophryne Mehely (1901) p. 177

Pomatops Barbour (1910) p. 89

Phrynomantis Zweifel (1972) p. 460

Diagnostic definition: As above for the tribe Phrynomantini.

Content: P. boettgeri (Mehely) 1901; *P. doriae* (Boulenger) 1888; *P. dubia* (Boettger) 1895; *P. eurydactyla* Zweifel, 1972; *P. fusca* Peters, 1867; *P. glandulosa* Zweifel, 1972; *P. humicola* Zweifel, 1972; *P. kopsteini* (Mertens) 1989; *P. slateri* (Loveridge) 1955; *P. stictogaster* Zweifel, 1972; *P. wilhelmana* (Loveridge) 1948.

Remarks: I have not seen *P. boettgeri, P. dubia, P. glandulosa* or *P. kopsteini.* While it is likely that the first three species are correctly assigned to *Phryno-mantis,* the large subarticular tubercles and narrowly separated maxillae of *P. kopsteini* (Zweifel, 1972) indicate that it may be more appropriately assigned to *Mantophryne.* Two subspecies of *P. humicola* (*P.h. humicola* and *P.h. compta*) have been described (Zweifel, 1972). I have added (above) characters emphasizing their phenotypic distinctness.

XENORHININI New Tribe

This tribe accommodates the genera *Xenobatrachus* and *Xenorhina.*

Diagnostic definition: (1) two supplementary slips to *M. intermandibularis* from the ventral margin of angulosplenial, posterior inserting on median aponeurosis; (4) *M. geniohyoideus medialis* absent; (5) *M. geniohyoideus lateralis* arising from mandible only; (6) *M. genioglossus basalis* with cultriform posterior projection; (8) three *Mm. petrohyoidei posteriores;* (9) *M. petrohyoideus posterior* III arising from exoccipital and otic ramus; (10) *M. depressor mandibulae* lacking origin from anterior 1/2 of ventral margin of typanic ring; (11) origin of *M. depressor mandibulae* from otic ramus broad, well developed; (12) *M. adductor*

mandibulae posterior longus segmented, bearing superficial tendon of insertion; (13) anterior origin of *M. adductor mandibulae externus superficialis* from fascia; (14) *M. longissimus dorsi* not inserting on dorsal fascia; (16) *Mm. transversi abdominis* and *obliqui abdominis externi* terminating on ventral abdominal aponeuroses; (17) two sites of insertion of *M. serratus medius;* (18) origin of *M. levator scapulae inferior* partly from first three vertebrae; (19) deep slip of *M. pectoralis sternalis* well developed; (20 medial slip of *M. lumbricalis brevis digiti* IV of manus cylindrical, arising from centrale postaxiale; (22) *M. tibialis anticus brevis* arising relatively proximally; (23) *M. opponens hallucis* arising from a distal tarsale; (24) *Mm. lumbricales breves digitorum* IV and V of pes fused along much of length; (25) frontoparietals 3× as long as broad; (30) median expansion of vomero-palatine well developed; (32) cultriform process of parasphenoid broad; (37) dorsal surface of otic ramus continuous with anterior surface of medial flange of squamosal shaft; (38) maxillae meeting anteriorly, no ridge on snout; (39) mesial expansion of anterior margin of palatine shelf of maxilla well developed; (4) anterior margin of nasal capsule not calcified; (42) humerus curved, crest well developed; (45) ilium bearing moderately developed dorsal crest; (46) direct ligamentous attachment between ilium and sacrum; (47) eye small (E: S-V < 0.090 usually); (48) subarticular tubercles absent or poorly developed; (51) surface of posterior part of tongue bearing deep longitudinal striae; (53) posterior pre-pharyngeal fold bearing few denticles (usually < 10).

Of these states, (6), (11), (39) and (51) are peculiar to the Xenorhinini among the Asterophryinae.

GENUS *Xenobatrachus* PETERS and DORIA 1878

Xenobatrachus Peters and Doria (1878) p. 432

(type species *X. ophiodon* Peters and Doria)

Choanacantha Mehely (1898) p. 175

Diagnostic definition: (31) one or more spike-like odontoids on the vomero-palatine.

Content: X. bidens (van Kampen) 1909; *X. giganteus* (van Kampen) 1915; *X. macrops* (van Kampen) 1909; *X. mehelyi* (Boulenger) 1898; *X. obesus* Zweifel 1960; *X. ocellatus* (van Kampen) 1913; *X. ophiodon* Peters and Doria, 1878; *X. rostratus* (Mehely) 1898; *X. subcroceus* Menzies and Tyler, 1977.

GENUS *Xenorhina* PETERS 1863

Xenorhina Peters (1863) p. 82

(type species, *Bombinator oxycephalus* Schlegel)

Pseudengystoma de Witte (1930) p. 132

Asterophrys (part.) Parker (1934) p. 58

Xenorhina Zweifel (1972) p. 529

Diagnostic definition: As above for the tribe Xenorhinini.

Content: X. bouwensi (de Witte) 1930; *X. minima* (Parker) 1934; *X. oxycephala* (Schlegel) 1858; *X.*

parkerorum Zweifel, 1972; *X. similis* Zweifel, 1956.

Remarks: This is a paraphyletic genus closely related to *Xenobatrachus*.

ACKNOWLEDGMENTS

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